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Ecology of Western Masailand, East Africa

By

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Lee Merriam Talbot
A.B. (University of California) 1953
M.A. (University of California) 1963

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

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UNIVERSITY OF CALIFORNIA

Approved:

Carl O. Sauer

A. Starker Leopold

Harold F. Heady

Committee in Charge

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PREFACE

121 Grasslands cover much of the earth's land area. They occur on many soil types and in several climatic zones. Some are open prairie or steppe and others include woody growth ranging from scattered bushes to open woodland. Grasslands are classified in many ways. Foresters classify them from the standpoint of the woody vegetation they contain, range specialists from the grasses, and zoologists from the animal life. The unifying factor is the grass cover. It, however, is only one of the interrelated factors, which include other vegetation, animal life, climate, fire, man and soils, which together form the grassland ecosystems.

Grasslands and their edges have supported the most abundant and varied populations of larger wild animals found on each continent. They also provide rich grazing land for domestic livestock and many are suitable for other types of agriculture. As the human population has expanded, grasslands have been among the first -- and most thoroughly -- exploited areas. Although grasslands remain, the former grassland ecosystems have almost totally disappeared. The two principal factors involved in this change have been removal of the animals from the former ecosystems, and

121 modification of the environment.

The larger fauna of grassland ecosystems normally included both ungulates and predators. The larger predators (Ursidae, Canidae, and Felidae) competed directly with man for both wild and domestic ungulates, and some of them were also a threat to man himself. Consequently they have been hunted intensively throughout history. The earliest documentated extermination is that of the European lion (Leo leo subsp.) in A.D. 80-100, and over half of the species of mammals exterminated in historical times in Africa, Asia, Europe, and North America have been larger predators (Harper, 1945).

The larger grassland ungulates required extensive feeding grounds, thereby competing with man and his domestic livestock, and they were a source of food and other animal products useful to man. Therefore these animals as well as their predators, were subjected to early and intensive pressure from hunting and habitat alteration. In America, for example, between roughly 1850 and 1890 the American bison (Bison bison) was reduced from a population estimated in the millions to about 1,000 animals (Allen, 1942). About 40 per cent of the total mammal species exterminated in Asia, Europe, Africa and North America were these larger ungulates

121 (Harper, op. cit,)

Other components of the former grassland ecosystems have also been affected. Maintenance of such ecosystems with their ungulate populations required large areas. Increasing human land use has left few significant areas of grassland undisturbed. As Darling (1956) has emphasized, most of the wild lands of the world have been significantly modified by domestic livestock. Changes in the fire regime, diversion of water supplies, cultivation, and other human activities have affected the vegetation, soils, and water as well as the other component parts of the grassland ecosystems.

As a result it is rare to find an example of the former grassland ecosystems with its fauna intact anywhere in the world. There is a large body of scientific information about existing, modified, and often managed grasslands, but there is very little such information on the former, complete grassland ecosystems. Study of such relic situations would provide information necessary for effective management of the areas themselves, but possibly of greater significance, such information might aid to understanding more about the ecological processes, past and present, in now-modified grasslands in other parts of the world.

121 This paper describes and analyses the ecology of such a relic grassland ecosystem.

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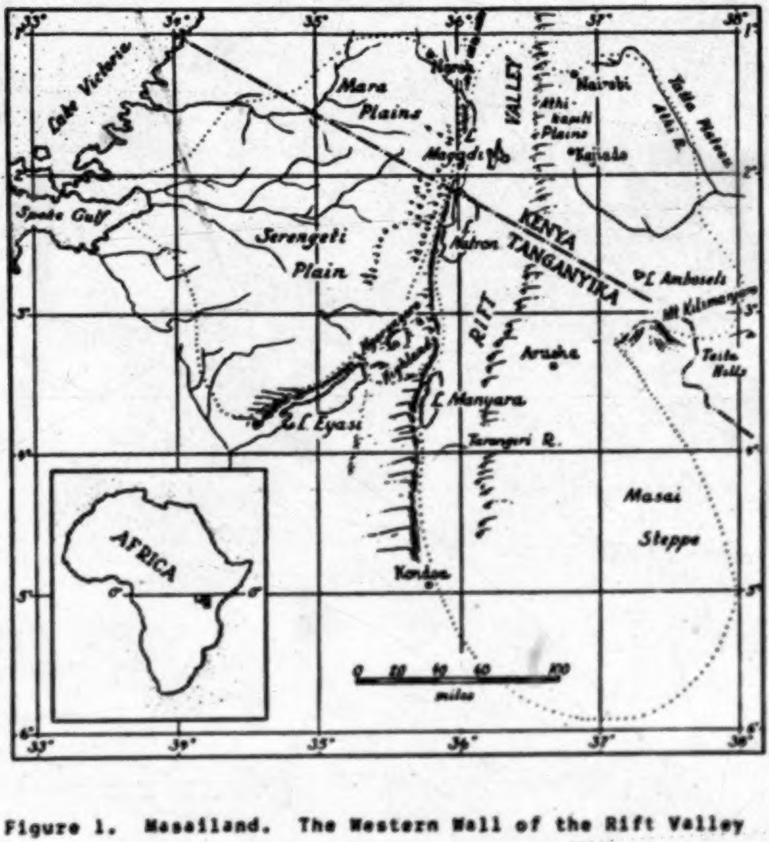
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Speke Gulf
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L. Eyasi
Tarangire R.
Masai Steppe
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Figure 1. Masailand. The Western Wall of the Rift Valley Divides Western Masailand from Eastern Masailand.

INTRODUCTION

121 Within the past century the grassland ecosystems of Africa have been as much altered as those of the rest of the world. The assemblages of plains wildlife of which Roosevelt (1910) wrote in such wonder have now almost disappeared. One area, however, has remained largely unaffected by "progress."

101 *133 [131] The Serengeti-Mara region covers some 20,000 square miles of open or wooded plains land, rolling hills and flat prairies, lying across the Kenya-Tanganyika border just east of Lake Victoria. Most of the region lies in Western Masailand, and much of the part outside the Masai land unit is in Tanganyika's Serengeti National Park.

Topographically Western Masailand is well protected. The Great Rift Valley forms the eastern boundary of this region, and on the south the Rift plus the Ngorongoro Highlands provide a barrier; the north is protected by the Mau Escarpment, and on the west the Siria Escarpment and Lake Victoria form a discontinuous but effective boundary (Fig. 1).

101 The Masai tribe has provided the other major protection. Before the White Man arrived -- but only just

101 before -- the Masai tribe occupied what is now Western Masailand by conquering and evicting the previous [176] residents (Grant, 1957). The Masai were a fierce and warlike people. Once they had taken over that country no one seriously disputed it with them.

175 648 In the early 1900's through the Government of Kenya the Masai made a treaty directly with the Queen of England. This involved re-settling a segment of the Kenya Masai, but the long term effect was to put the Kenya Masai in a privileged position relative to the other tribes -- who did not have such a treaty -- and to give them a degree of autonomy virtually unknown in other parts of Kenya. Because of their remote location and the nature of the Tanganyika Administration, the Masai in the Tanganyika portion of Western Masailand also maintained [177] a large degree of autonomy. Aided by these circumstances, [178] the extremely conservative western Masai have kept largely to themselves, and to an extraordinary degree the modern world has gone on around them, instead of over them and through their country.

121 *122 *[114] My first visit to the Serengeti-Mara Region was in 1956. I had been assigned to carry out a brief ecological reconnaissance of the Serengeti National Park under the sponsorship of the Wildlife Management Institute and the American Committee for International Wild Life Protection (Talbot, 1956).

12.1 In 1954 and '55 I had traveled through other parts of Africa, the Middle East, and southern Asia (Talbot, 1960a) working as Staff Ecologist for the International Union for the Protection of Nature (now International Union for Conservation of Nature and Natural Resources). Many of the areas I visited were arid or semi arid steppe or desert lands with impoverished vegetation and soil, and little if any wild life. Within historical times many of these areas had supported grassland with grassland wildlife. Yet these grasslands were history, and little or no direct evidence remained of the processes that operated in and maintained the former grassland ecosystems in those vast areas. Even in North America in spite of the voluminous writings about the American Prairie with its buffaloes, relatively little scientific information is available on its ecology. Therefore a look at an undisturbed grassland ecosystem anywhere in the world would be much like a look back into history.

Western Masailand provides this experience.

*114 When I entered the region in 1956 I came from the south. My first view of the Serengeti Plain was from the *133 Ngorongoro Highlands. From the foot of the mountain slopes, 2,000 feet below, the level expanse of the plain stretched to the far horizons, unbroken except by occasional low hills and scattered granite kopjes.

*13 Acacia trees followed watercourses a little way into the plain, then gave way to open grassland. Later, driving across the center of the plain, the grassland appeared endless and the only landmarks were the peaks of the Ngorongoro Highlands floating above the heat haze 50 miles behind. In one place the plain was empty and dry. A few miles farther on rain had fallen and the grassland was green and alive with herds of antelopes and zebras with their attendant predators and scavangers. Watching this scene one felt that ~~he~~ was looking back into history. The head-heavy wildebeests could have been bison on the American Prairie; Zebras and gazelles, nervously watching a lion, could have been their nearly extinct relatives on the Syrian Plains.

121 When I left the Serengeti in 1956 it was with the firm intent to learn all I could about this place of living history. Subsequent search for reference materials in Europe, England, and North America showed that there was very little known about the area. In fact there were very few scientific data applying to any phase of the East African grassland ecosystems. It appeared that the Serengeti-Mara Region was an almost virgin field for ecological research.. The possibilities were tremendously exciting.

*122 *(114) Three years later, in June, 1959, I was fortunate enough to return to East Africa with my wife to carry out a study of the Serengeti-Mara Region. This visit was initiated under the Foreign Field Research Program of the National Academy of Sciences-National [illegible]earch Council and subsequent extensions were made [illegible]e by the New York Zoological Society and the [illegible]ent of Kenya.

In the process of this study I have spent 34 months in East Africa: January through March, 1956; June 1959 to December 1961; and March into May, 1962. Most of this time, about 30 months, was spent in field research. My wife was with me throughout the major period of field research, from June 1959 through December, 1961.

121 The objectives of the study were to define, analyse and explain as many as possible of the interrelationships between the various species of wild animals, the vegetation, soils, climate, and the Masai with their livestock.-- i.e. to describe the ecosystem and to define the roles of its component parts.

To avoid too great dispersion of our efforts in wildlife research, we decided to concentrate our initial efforts on one important species. From the standpoints of biomass, migrations, predation, contact with man, and

121 impact on the landscape, the Western White-Bearded Wildebeest (Gorgon taurinus hecki) appeared to be the most important single species in the plainsland complex. Initial study of this species promised to yield more information of importance to the whole plainsland complex than would the study of any other species.

128 When we returned to California and began compiling the field data we found voluminous material on the wildebeests and on many of the associated species as well. It was clearly not within the scope or purpose of the present paper to include all the detailed and extensive wildlife data. Consequently, these data are presented below essentially in summary form but in as much detail as is required to accomplish the purpose of this work. More detailed wildlife studies are being presented elsewhere (Talbot and Talbot, 1963b).

121 This paper, then, presents what I have learned about the ecology of Western Masailand. It is essentially a description and analysis of a relic grassland ecosystem,

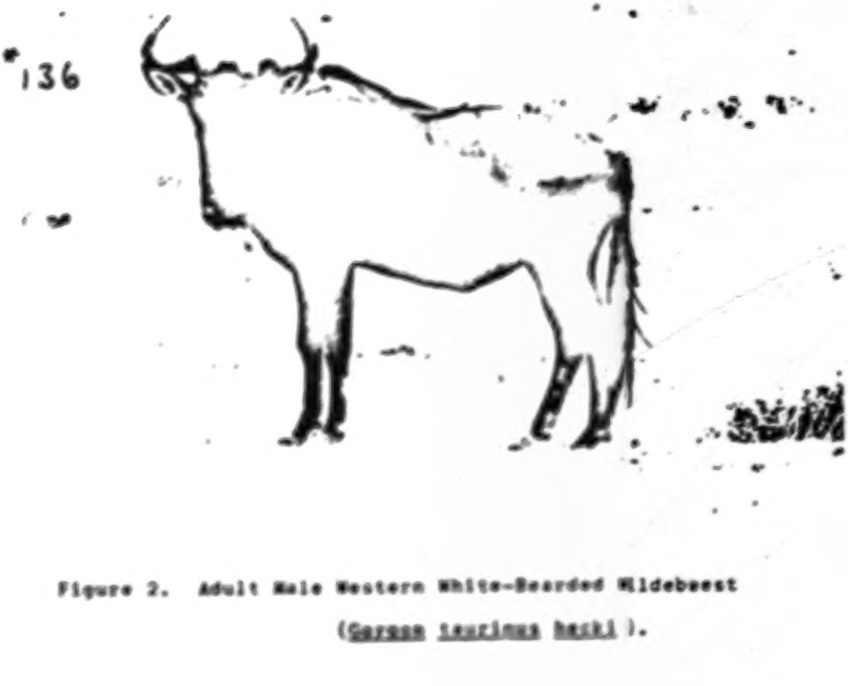

Figure 2. Adult Male Western White-Bearded Wildebeest (*Gorgon taurinus hecki*).

PRESENTATION AND DEFINITIONS

128 An ecological study is difficult to organize for presentation, since all the component parts are interrelated. The problem is to find a starting point. This difficulty is emphasized in a study as broad as this one. The form that has been adopted is as follows:

1. To provide a general description of the area and its significance to this type of study.
2. To describe, in turn, the various component parts of the ecosystem, treating each component separately but defining its relationships with the other components.
3. To bring the components together with a discussion of the nature of the ecosystem and its historical implications.

Methods used in the field collection of data are mostly described where appropriate in the text. The basic methods that apply to the entire study, however, do not belong in any one section, and these are described in the chapter on Compilation of Data.

101 Masailand is the term normally used in East
131 Africa to denote the Masai administrative land unit,
which includes about 15,000 square miles in Kenya and
*136 some 23,250 square miles in Tanganyika. The term
*137

*136 *137 normally connotes perennial Themeda grasslands with scattered trees and with populations of wild grassland ungulates, largely because most of the areas in Kenya and Tanganyika where these conditions are still found are in the Masai land units.

*133 The Great Rift Valley passes through Masailand lying roughly on a north-south line (Fig 1). Where it passes through the northern part of Masailand, the eastern wall of the Rift is precipitous, often rising vertically from one to two thousand feet above the Rift floor. The eastern wall is generally far less precipitous, rising in a series of faults which grade into a long uneven slope in the south. Throughout most of its length in Masailand, the western wall of the Rift is an effective barrier to most animal movement, and much human movement. For much of its length the wall is the boundary between the different sections of the (128) Masai tribe. As discussed below, the areas of Masailand east and west of the Rift are at present distinct ecological units. Consequently, I have divided Masailand into eastern and western sections, using the west wall of the Rift as the dividing line (Fig. 1).

Eastern Masailand, then, includes the Masai land unit in and to the east of the Rift, and Western

133 Masailand that to the west of the top of the western escarpment of the Rift.

101
133 The boundaries of Western Masailand, as the term is used here, are ecological and not political (Fig. 2). In Kenya, the Masai land unit includes much of the southern face of the Mau escarpment, a forested massif rising 4,000 to 5,000 feet above the Masai plains. Ecologically, much of the higher Mau forest area does not belong in the present discussion and it is not included. The same is true of part of the Ngorongoro Highlands in Tanganyika, and some of the administrative Masailand in Kenya above the Siria Escarpment.

128
101 Included within Western Masailand is the Serengeti National Park in Tanganyika and its western environs (Fig.2). Politically this area is not at present in the Masai land unit, but from the standpoints of physiognomy and ecology it is homologous with the adjoining Masai land unit.

128
101
133 The Serengeti-Mara Plains Region refers to non-mountainous parts of Western Masailand. Although neither a plain nor a plateau in the strictest geographical sense (Kendall, Glendinning and MacFadden, 1951), this area is relatively flat and takes its name from the

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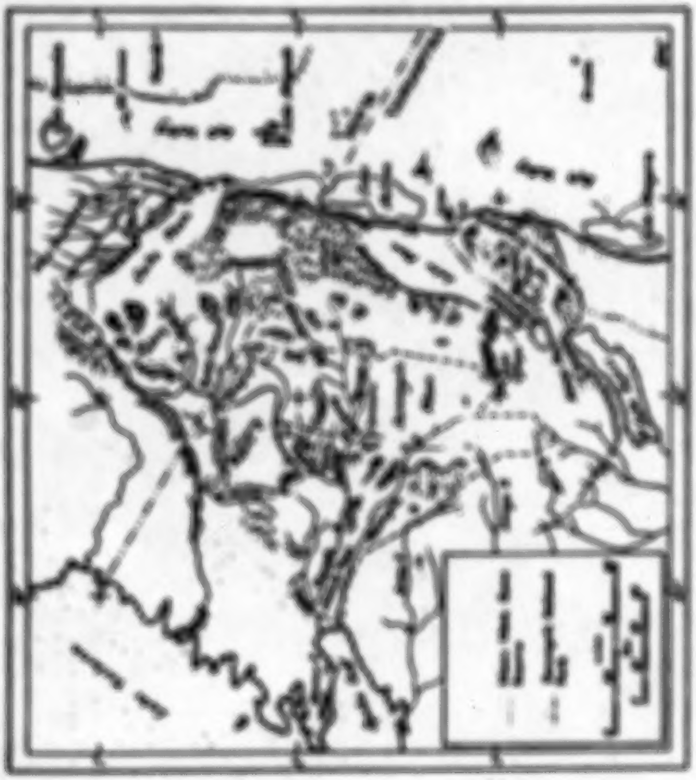

Figure 3. Physical Map of Western Masailand.

Fig
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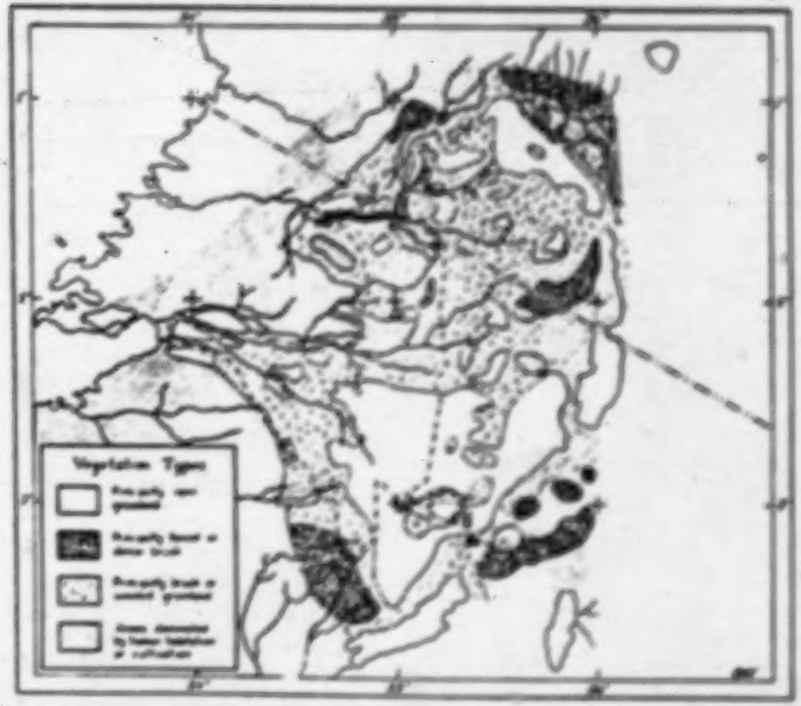
Vegetation Types

Figure 4. Vegetation Types of Western Maasailand.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

128 Serengeti Plain of Tanganyika and the Mara Plains of
101
133 Kenya. The region includes these areas, plus the homologous habitat between and around them, and covers around 12,000 square miles.

121 The study area included the plains region and
128 its surroundings in order to define the boundaries of the ecological unit. The total area studied covered roughly 20,000 square miles.

I have used the term *grassland* in a very broad sense. Within the climatic and edaphic ranges of grass (which includes much of the world), virtually all areas are grasslands or potential grasslands. Grasses and associated forbs provide the larger part both of the food for the wild and domestic grassland animals, and of the fuel for the fires. By manipulation of fire, grazing, and other factors the grass composition and vegetation physiognomy of a given area may be altered considerably; but within that area the maximum biological productivity appears to be achieved by a given combination of grasses. This combination represents a response to the various factors in the ecosystem, and it is constant in a given area, while varying from area to area, as do various factors in the ecosystem. *Themeda triandra* is the dominant grass of some grassland ecosystems in

(2) East Africa, while various species of *Hyparrhenia* are (2) dominant in those of other areas. Heady (1960) classified and mapped the grassland and potential grassland types in East Africa essentially on this basis, as did Rattray in mapping the grass cover of Southern Rhodesia (1957) and the whole of Africa (1960).

(2) In this work I am using the term *ecosystem*, defined by Dice (1952), as "an ecologic community together with its habitat."

Where physiognomic descriptions are necessary, I have used those standardized by the Scientific Council for Africa South of the Sahara (1956).

SIGNIFICANCE OF WESTERN MASAILAND

(2.1 4 13 Between the deserts, tropical rain forests, and mountain masses in Africa there are broad belts of savanna, steppe or prairie grasslands. These belts were mapped clearly by Shantz and Marbut in 1923, and more recently by Rattray (1960). In general terms, one belt crosses northern Africa passing between the Sahara and the rain forests of the Congo Basin and the lands adjoining the Gulf of Guinea. Another belt passes south of the Congo Basin and north of the Kalahari Desert. A third belt runs along the east coast of Africa from the Union of South Africa north to the Sahara. The three belts are more or less continuous, joining in the region of East Africa. Masailand is in the center of this junction area.

12.1 4 137 •136 Tall grass savanna, dominated by genera of tall grasses such as *Hyparrhenia*, occurs primarily along the wetter edge of the northern belt. When the grasses in this type of savanna are low and sprouting they can provide forage for many ungulates. But when they grow tall and coarse only a few animals, such as buffalo(1)

---

(1) For the scientific names of the mammals of Western Masailand see below, the chapter on Wildlife.

121 *134 *137 and elephant can use them. Therefore, where this type is very extensive, the biomass of wild ungulates it supports is relatively low. Much of this type of savanna is derived from forest lands originally cleared for cultivation (Rattray, 1960). This tall-grass savanna is not represented in Masailand.

Tall and short grass steppes and savannas are found throughout the African grassland belts, and all are represented in Masailand. These areas provide yearlong grazing of high quality. In eastern Africa (East Africa and the eastern Congo) these areas support the highest known biomasses of wild ungulates in the world (Bourlière, 1963; Talbot and Talbot, 1963a).

121 *13 Therefore, the grassland ecosystems of Masailand are typical of the most productive of such ecosystems in Africa. As noted above, however, few such ecosystems remain in essentially undisturbed form. Most are modified in some degree. Western Masailand is an outstanding exception.

*133 Much of Western Masailand is above 5,000 feet elevation, while the bulk of Eastern Masailand lies 000 1,000 to 2,000 feet lower. Allowing a three degree F.

#132 Allowing a three degree F. average temperature decrease for each 1,000 feet rise in elevation above sea level (Heady, 1960), much of Eastern Masailand would have up to six degrees F. higher average annual temperatures than Western Masailand. Over the greater part of both areas the mean annual rainfall is similar, with Western Masailand receiving roughly 30 inches while Eastern Masailand probably receives some 25 inches (Met. Dept., 1959).

#13 Except for the Rift floor, the vegetation types
184 and communities in both areas appear to have been much
182 the same (Edwards, 1951:32; Edwards and Bogdan, 1951:3; Heady, 1960:12, et. seq. and his appended map of Grasslands and Potential Grassland Types). However, Eastern Masailand with lower rainfall and higher temperatures would be more vulnerable than the western area to desiccation through human activities, especially overgrazing, overburning, and diversion of water supplies.

As noted above, Western Masailand has been little affected by recent changes in human activity. On the other hand, Eastern Masailand has been intensively modified in the past fifty years or so. Much of Eastern Masailand is easily accessible by road and railway. Nairobi, capital of Kenya, lies at the northern end of Eastern Masailand. Nairobi was started in 1899

#13 182 184 as a base camp for construction of the Uganda railway. Today it is a modern city of about 250,000 people. Spreading south and east from the city along the edge of Masailand are fenced ranches and farms. The Great North (Cape to Cairo) Road runs dustily through Eastern Masailand. Arusha, virtually surrounded by Masailand in northern Tanganyika, is a provincial capital and the center of a flourishing farming district. The provincial headquarters for the Masai Administration in both Tanganyika and Kenya are situated in Eastern Masailand.

The Masai living east of the Rift are from different sections of the tribe than those living to the west, and they are significantly less conservative. Consequently Eastern Masailand has received more ranching schemes, water holes and other projects to "improve" their livestock grazing than Western Masailand, and therefore Eastern Masailand is far more seriously overgrazed. Over much of the area vegetation is impoverished and surface conditions show severe desiccation.

12 #13 #2.13 It is difficult to obtain quantitative data on the numerical increase in livestock or its impact on the vegetation, since such data from earlier years are not generally available. One area where such data

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

12 *13 *233 are available will serve as an example.

12 *13 175 *233 Passing north from Arusha, the Great North Road skirts Mt. Meru, then crosses about 40 miles of fairly level land before passing Longido Hill, 14 miles south of the Kenya border. In German times (prior to 1918) the land from here westward into the Great Rift was maintained as a game reserve and Masai were excluded. From the descriptions of East African residents who visited the area during and just after the 1914-1918 war, and from the description and vegetation map of Jaeger (1913) this area was open perennial __Themeda__ grassland, with good grass cover and abundant wildlife.

The British took over Tanganyika as a Trust Territory after World War I, and in the 1920's they 12 *13 *233 182 opened the reserve to the Masai. For a time the Masai had moderate numbers of livestock, grazed seasonally in the area along with the wild ungulates. Then a series of water points were provided, using bore holes and piping water into the grassland from springs on nearby wooded mountains. This water allowed the Masai to keep their cattle year-long in areas formerly used only seasonally, with the result that most of the area has been devastated. The __Themeda__ with the rest of the perennial grass cover is gone. The soil is gone, leaving

12 *13 *233 1#2 erosion pan and blowing sand and dust. Thorn bush has invaded the area and the aspect at present is of an open thorn bush wasteland with virtually no herbaceous ground cover. One vestige of the former grassland remains. At mile 29 from Arusha, the road passes through a roughly half mile wide strip of open perennial grassland. This is the bottom end of a European ranch where grazing has been strictly controlled.

*13 #2 *233 The grazing-induced devastation seen in the above example is repeated, in greater or lesser degree, throughout Eastern Masailand.

The wildlife in Eastern Masailand has been severely affected by this recent land abuse. Diversion of water to the Masai water points has denied the wild animals many of the sources of water they previously relied upon during the dry seasons. Of the seven or eight major dry season water supplies that existed in Eastern Masailand in Tanganyika, less than 20 years ago, only two remain at present (Talbot, Talbot, and Lamprey, 1961). Overgrazing by domestic livestock has altered or removed the grass cover which provided much of the food supply for the wild ungulates. The overgrazing-induced change from grassland to thorn scrub rendered much of the habitat unsuitable for the open

#17 182 #231 [417] grassland species. Fences have further restricted the movements of the migratory species.

The impact of recent land use changes on wildlife in Eastern Masailand can be illustrated by the wild ungulates of the Athi-Kapiti Plains. This _Themeda_ grassland lies immediately south of Nairobi, in Kenya's Eastern Masailand. Fifty years ago, in terms of climate, soil, vegetation, elevation, and animal life, this area was virtually identical with Western Masailand, 60 miles airline to the west. Here, as in Western Masailand, the wildebeests are considered the key ungulate species, and they will serve as an example:

#136 Until about 1927 the wildebeest population spent the wet seasons on the Athi-Kapiti Plains and in dry seasons moved north, east, and south (Kenya Game Dept., 1908-1914, 1920-1921, 1925, 1927; Percival, 1928; Simon, 1962). From the above references and discussions with local residents and game authorities, especially the Hon. M.H. Cowie, Director of the Royal National Parks of Kenya, Mr. S.I. Ellis, Warden of Nairobi National Park, and Captain D.R.P. Zaphiro, Game Warden of Kajiado District, the wildebeest populations and movements in Kenya east of the Mara area, prior to the 1920's appears to have been as follows: There presumably were two main populations: one centered on the

*136 Athi-Kapiti Plains in the wet season; another larger population centered on the plainsland north of Mr. Kilimanjaro in the wet seasons. These two populations were migratory in the sense described below moving to water in the hills and bush country during dry seasons, and returning to the plains during the rains. There appear to have been some intermingling and possible interchange of population between the northern and southern populations. In extremely dry periods many of the northern animals moved south, and much of the Kenya population moved south into what is now Tanganyika. In addition to the two main migratory populations there were apparently some relatively localized populations, such as one north of the Thika River and another near Juja (both north-east of Nairobi), which in most years apparently did not take part in the general movements.

There were wildebeests in the Rift Valley from the Tanganyika border north to the Kedong, and in the early 1900's at least, they extended to the south shore of Lake Naivasha (Meinertzhagen, 1957). The relation of these animals to the wildebeest population west of the Rift is discussed below. There is no absolute barrier to movement of wildebeests between the Athi-Kapiti Plains and the Rift west of Kajiado, although we have never observed wildebeests on such steep, rough terrain.

*136 In times of stress some zebras have been noted making such a movement (Kenya Game Dept., 1962), but we have no recent evidence of any such moves by wildebeests.

The population of wildebeests on the Athi-Kapiti Plains apparently had access to all of the area occupied by wildebeests in Kenya east of the Rift, and they may have moved south into Tanganyika. The southern part of this area, however, was only visited in times of drought. The normal non-drought range for these animals probably covered roughly 3,400 square miles. The present range is only some 20 per cent of the former range. It represents the former wet season range for the wildebeests. With the exception of the watercourses in Nairobi National Park and part of the Athi River, there are no dry season water supplies or grazing grounds left accessible to the Athi-Kapiti wildebeests.

*136
122 According to Game Warden Zaphiro, the population of wildebeests in the southern area now appears less than that of the Athi-Kapiti Plains. Severe overgrazing by domestic livestock and diversion of water have rendered much of the area unsuitable for wildebeest habitat. Since the early 1900's, much of the area on both sides of the border that was open perennial grassland has been turned to near desert or waterless, sandy, thorn scrub

*13C
17L (Talbot, Talbot, and Lamprey, 1961).

The wildebeests in Western Masailand represent a population under essentially undisturbed conditions while those in Eastern Masailand are a population surviving under conditions much altered in the past half century. As described below this situation appears reflected in differences between the two populations, especially in population dynamics and behavior. Comparison of the data in this report and Talbot and Talbot, 1963b with the results of ecological studies in Eastern Masailand could yield significant information on the differences between disturbed and undisturbed grassland ungulates.

The area occupied by these wildebeests is about 950 square miles. It is now considered a closed habitat for the wildebeests (Zaphiro, 1958) being bounded by the Rift wall in the west, bush country and grazing schemes to the south, hills, fenced farms and the city of Nairobi on the east and north. Therefore the wildebeests are unable to migrate to seek their preferred forage when the grasses in their present restricted range dry. And the grasslands that are available to them have been altered by overgrazing.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

#136 As will be discussed in greater detail below, several lines of evidence show that the wildebeests on the Athi-Kapiti Plains are surviving under more or less severe nutritional stress. The most dramatic evidence, however, comes from the impact of the 1961 drought. Prior to the drought there was a population of some 9,000 wildebeests on the Plains (Kenya Game Dept., 1962). During the severe drought of 1961, about 25 per cent of these animals died (Ibid.), while there was no such mortality in Western Masailand where the wildebeests had freedom of movement to follow their requirements for optimum food and water. Before the drought in the Athi-Kapiti Plains the biomass of the three key ungulate species -- wildebeest, zebra, and kongoni -- was about 7,520 pounds per square mile; this biomass had dropped to 3,525 pounds per square mile after the drought due to death and possibly some emigration (Kenya Game Department, 1962). During the same period the biomass of these three species in Western Masailand remained at about 16,890 pounds per square mile.

#13 The Isolation of Western Masailand

Western Masailand appears to have been long isolated from Eastern Masailand, and the topographic and ecological barriers surrounding the area seem to have #136 been very effective (Fig. 3 and 4). There is some

#136 movement of elephants between the Western Masailand and the forests or highlands to the north, west and south. A few buffalo and possibly some of the other bush dwelling species may occasionally pass in or out of the area. But most of the ungulates, including all of the "plains game" are resident.

Evidence that this separation is of long standing comes from the races of the ungulates themselves. The wildebeests of Western Masailand are the Western White-Bearded Wildebeest (Gorgon taurinus hecki), while those in the bottom of the Rift, near Lake Natron and Lake Eyasi, are the eastern race, Gorgon taurinus albojubatus (Brooks, 1961; Roosevelt and Heller, 1914; Swynnerton and Hayman, 1950; Talbot and Talbot, 1963b). The same sharp division holds true for races of he Thomson's gazelle and other antelopes (Ibid).

To the north and south the forested Mau Escarpment and Ngorongoro Highlands appear as absolute barriers to movement of grassland ungulates. The Siria Escarpment on the northwest is partially backed up by a dense forest in the north and by a dense human population further south. When the human populatin was lower there may have been movement across the Siria by bush animals, but apparently not by the grassland species. The shores of Lake Victoria have long been occupied by dense human populations supported by the abundant fish of the lake and the well watered agricultural land nearby. Movement of these people eastward into Masailand has been restricted by tsetse flies which carried both human and animal trypanosomes, and by the Masai within the past two centuries.

The one area where in historic times there was a significant break in the barriers of Western Masailand is in the northeast corner. The races of Thomson's gazelle, wildebeest (Fig. 5), and kongoni that were found in Western Masailand, were also found in the Kedong region of the Rift near Mt. Suswa, and northwards (Roosevelt and Heller, op.cit.). Wildebeests, as an example, were found in the Rift north and west of Nairobi at least until the time of the first world war. Meinertzhagen (1957) records them as being found on the south shore of Lake Naivasha in 1902. Roosevelt and Heller (1914) showed wildebeests occupying the center and west of the Rift in the vicinity of Mt. Suswa just south of Naivasha in 1909 and 1910, and Percival (1928) noted their distribution slightly earlier as extending to the East Rift Wall (near the present Kijabe). The animals involved were definitely the western form and not the

[TEXT CONTINUED ON PAGE 35]

19: Talbot K-4,5 (1956-1962)1964 FL.12 Masai FL.12

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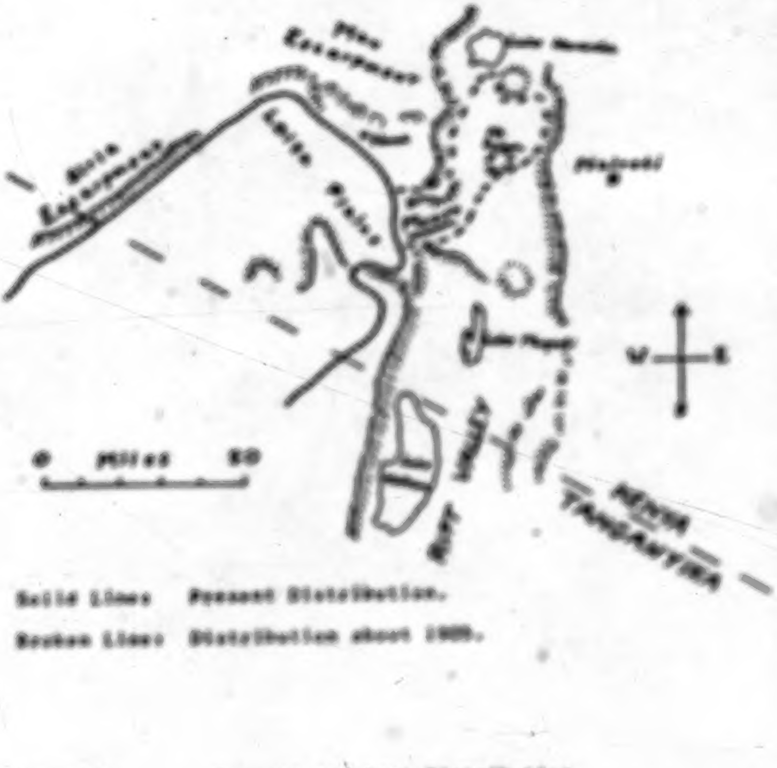
Mau Escarpment
Siria Escarpment
Loita Plains
0 Miles 20
W
E
KENYA
TANGANYIKA

Solid Lines: Present Distribution.

Broken Lines: Distribution about 19[illegible].

Figure 5. Present and Past Distribution
of the
Western White-bearded Wildebeest

*136 eastern, since Roosevelt and Heller collected some of the specimens here from which they described the difference between the two races.

At that time the link between the wildebeests in the Rift and those in the present Serengeti-Mara region may have been the Mosiro Plateau. In that area there is not the sheer wall that characterizes much of the western edge of the Rift. Instead there are a series of steps and slopes which by themselves would not prove a barrier to wildebeest movement. *13 [167] Old Masai living on the Mosiro Plateau told us that they remembered seeing wildebeests on the Plateau when they first moved there (about 45 years earlier), and at that time the plateau country was open with tall grass, no gullies and no brush. Today the Mosiro area is one of the most severely overgrazed parts of East Africa, and is largely bare of grass, deeply eroded, and covered with thorn scrub (Talbot, 1964b). We regard it in its present condition as an effective barrier to movement of wildebeests.

*136 Roosevelt and Heller (op.cit.) also mapped wildebeests of the western race south to the west side of the Rift to Lake Natron. Today, however, the wildebeests at Lake Natron are the lighter colored, larger, eastern form. If Roosevelt and Heller were correct that

19: Talbot E-4.5 (1956-1962)1964 Fl.12 Masai Fl.12

*134 the western form was found at Lake Natron, it seemingly
[225] has been replaced by immigrants from the east. At the
(498) time of their visit the land to the south-east of Lake Natron was a German game reserve from which the Masai had been excluded. I have flown over that area and even today, after fifty years of Masai over-use, it appears perfectly feasible as a route of passage for large antelope, at least in the wet season.

Percival (1928) notes that an occasional old bull will "come up" -- presumably to the Kajiado area -- from the Rift near Lake Magadi, which is adjacent to the area mapped by Roosevelt and Heller.

To my knowledge, none of the Roosevelt and Heller party visited the Lake Natron area. The map must have been drawn from second hand reports representing the best sources of information available at the time. It seems probable, then, that the wildebeests in the Rift near Lake Natron were then what they are now, representatives of the eastern race.

If this were so, although the Rift wall precluded movement east, why did these wildebeests not move farther north? At present the Rift between the Natron area and the vicinity of Mt. Suswa is hot, waterless, forbidding

*136 to most kinds of life, and certainly a barrier to normal wildebeest movements. If this area were less desiccated in previous times, it probably would have been the only point of contact between the eastern and western races of wildebeest. The Roosevelt collections from the Suswa area, however, would indicate that there had not been significant mixing of the races there, implying that any recent contact would have been on a small scale and any significant connection had been in the far past.

*136 179 229 *233 182 (244) No wildebeests remain in the northern area of the Rift. There are fenced ranches now south of Lake Naivasha and in the Rift adjoining the Suswa area. The remaining wild animals (kongonis, gazelles, etc.) are hunted on some of these ranches as food for labor. It appears that after the former wildebeest population of this area became isolated from the populations farther west (through Masai overgrazing in the Mosiro area) it was gradually hunted out. Kongonis and Thomson's gazelles are still found in this area.

Summary

*13 122 Masailand is centrally located in the system of grassland belts of Africa. The grassland ecosystems of Masailand are typical of the most biologically productive

*13 121 and most widespread such ecosystems of Africa. While *13 121 124 most African grassland ecosystems, including those of Eastern Masailand, have been modified by changes in human activities, those in Western Masailand have remained largely undisturbed.

*13 12 124 Although separated by the Rift, Eastern and Western Masailand were ecologically identical when the first white men arrived less than a century ago. Therefore these two land units provide the "before" and "after" examples, the control situation and the modified one. From this situation one may describe: the factors in operation in the undisturbed ecosystem; those in the disturbed situation; the nature of the changes and the factors involved; and the rates of change.

*13 121 The ecological and topographical barriers around Western Masailand are sufficiently effective that the boundaries of the ecological unit appear to have been essentially the same since prehistoric times.

The study area, therefore, presents an opportunity to study as nearly an undisturbed primitive grassland ecosystem as it is possible to find.

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19: Talbot K-4,5 (1956-1962)1964 FL.12 Masai FL.12

PROCEDURES

121 This chapter outlines the methods and procedures that apply to the study as a whole. Methods that apply to a particular part of the study are placed in the appropriate sections of the text. A description of collection, examination and measurement techniques, for example, introduces the section on Wildlife.

Background

122 Much of the professional work I had carried out prior to my first visit to the Serengeti region applied directly or indirectly to the present study. This is especially true of the work on arid and semi-arid grassland ecology involving North Africa, the Middle East, and Southwest Asia, carried out from 1954 through 1956 in the capacity of Staff Ecologist to the International Union for Conservation (Talbot, 1960a). Following the first visit to the Serengeti several months were spent in Brussels, Paris, and London accumulating the material then available on East African ungulates.

Subsequently, further library search was carried out at the University of California at Berkeley, in New York, and Washington, D.C. En route to Nairobi in 1959 my wife and I visited New York, Frankfurt, and Entebbe to

121 discuss the project with the three workers who had most recently been in the general vicinity of the study area.

Field and Laboratory Procedures

122 Most of our time in Africa was spent in the study area. Approximately once each two months we drove to Muguga, the headquarters of the East African High Commission agriculture, forestry and veterinary research organizations. We were provided with office and laboratory space there and had access to the fine library and shop facilities.

Occasional visits were made to Nairobi, Arusha, and Narok for supplies and meetings. The trip from Nairobi (near Muguga) to the northern edge of our study area required a long day of hard driving in dry weather, and much longer -- if possible at all -- in wet weather.

In the study area we had access to a house belonging to the Veterinary Department in Kenya, and another in the Serengeti National Park in Tanganyika. However, the area was so large that we spent much time on safari camping with a tent.[7] Part of the time we had one African helper and part we travelled alone. Prior to our arrival there were no roads through the center of *[illegible] the study area. We travelled in a British Land-Rover which we modified for our requirements. For long periods in the more remote areas we carried extra food, water, etc., in a small two-wheeled trailer.

Cooperative Projects

On arrival in East Africa, before beginning the field work we contacted all the individuals or organizations whom we knew were interested in ecological work in the Serengeti-Mara region. In each case we explained what we were going to try to do, asked for any advice or suggestions, and inquired whether or not we might help them while we were in the field. Out of these initial contacts the following cooperative studies developed (details are given where appropriate in the text):

Disease and parasite studies with the East African Veterinary Research Organization and the Kenya Veterinary Department.

Food habits studies with the Fauna Research Unit of the Kenya Game Department.

Herbarium collections and identifications with the East African Herbarium.

Soil sample collection and analyses, and rumen sample analyses with the Scott Agricultural Laboratory of the Kenya Ministry of Agriculture.

*/24 Aerial wildlife census and population composition determinations with the Kenya Game Department and Wilken Air Services, Nairobi (Stewart and Talbot, 1962a, 1962b; Talbot and Zaphiro, 1960; Zaphiro and Talbot, 1961).

Meat production and carcass analysis studies with the Animal Husbandry Division, East African Agriculture and Forestry Research Organization (Ledger, Payne and Talbot, 1961; Talbot, Ledger, and Payne, 1961).

Land use surveys with the Narok District Administration and the Kenya Game Department (Talbot, 1960a).

Other cooperative projects involved a variety of subjects including mapping, game cropping (Talbot, 1961), and testing and development of field immobilization techniques (Talbot, 1960b, 1960c; Talbot and Lamprey, 1961; Talbot and Talbot, 1962b).

Check Sheets

*/25
*/26 To facilitate taking complete notes rapidly, in a form which allows easy extraction of data, we used a series of standardized check sheets in addition to journal notes. These enabled us to collect a vast amount of information on a variety of subjects. Check sheets were used to record data on captured or collected animals, plant collections, and land conditions; in vegetation and

*115 *114 soil mapping and surveying; in capture gun development; in analysis of the effect of fires; and in recording plant, animal, and climatic data from field strip transects. Examples of the check sheets are included as figures in the text where appropriate.

Observation

*116 Observations were carried out in two ways. Many valuable data were collected from prolonged observations of an animal or area while the observer remained in one spot, or occasionally followed an individual animal or herd. Hilltops were used for vantage points where available, and occasionally we stalked animals on foot [11] or by crawling through tall grass and brush. The most efficient blind, however, was the Land-Rover. East African animals generally pay less attention to an automobile than to a man on foot, and consequently it is possible to get much closer to most animals in a car than out of it (Fig. 6).

*115 *116 The other principal observational method used was the strip transect or "field transect" method. The study area is about the size of the states of Vermont, New Hampshire, and Delaware combined. Some of the wild ungulates migrate freely throughout the entire area. Others, domestic livestock, and the Masai make shorter

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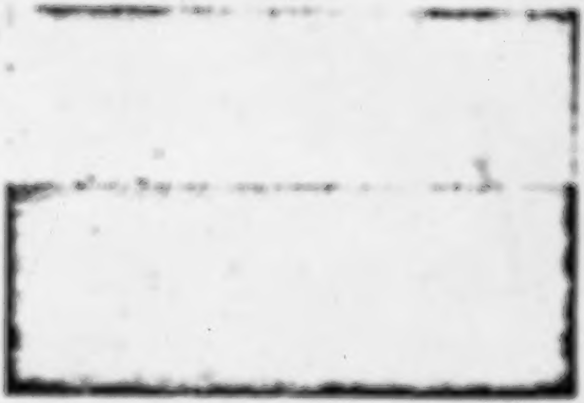

Figure 8.

Driving past a herd of wildebeest on the Serengeti Plain. Animals in the study area are little disturbed by a vehicle and visibility is generally very good.

*72.5 *72.6 migrations. Consequently, it was necessary to devise some method to provide a continual and representative sample of the whole area involved. At the same time, since we were dealing with an entire ecosystem, it was important to use uniform sampling methods for the various component parts of the system, so that the data on vegetation, for example, could be compared with that on animals (Riney, 1956). The method we developed was a variation of the King strip census (Leopold, 1933), closer to variable strip methods proposed at Nakuru (Worthington, 1954) and used, with variations, to determine sex ratios and population densities in the Albert Park in the former Belgian Congo (Bourlière, 1958; Bourlière and Verschuren, 1960:30, et. seq.). Most wild animals in the study area have no fear of a vehicle, so disturbance off the strip and flushing angles and distances were not problems (Webb, 1942; Davis, 1960; Hayne, 1949; Robinette, et. al., 1954, 1956). For the same reason, and because the visibility was usually good and the numbers of animals involved was great, it was neither practical nor necessary to measure the distance from the observer to each animal seen as in the strip counts of Dasmann and Mossman (1962). Instead, we observed a strip centered on the vehicle and extending a predetermined distance on each side. In addition to the animals, this then gave us a fixed strip

*125 *124 for sampling vegetation and other habitat factors. The width was usually set at a convenient multiple of a mile, and was altered somewhat depending on the type of cover. Occasional practice in shooting, especially with capture guns, assured that we could accurately estimate the strip edges. As an additional check, we often would pace off the distance involved, especially when entering a different type of habitat.

*125 All animals on the strip were recorded on a field transect check sheet (Fig. 7), usually by my wife, as we drove along. The herd compositions by numbers, sex, and age were noted, along with observations on their associations, behavior, movements, etc., and with notes on weather, fire, stage of growth of the vegetation, availability of water, time of day, and landmarks. Standardized abbreviations were used for speed and conciseness. Each strip was plotted on the maps of the region which we had previously compiled. Since no very accurate maps of the area were available, we made our own maps using aerial photos where available and plane table methods elsewhere.

The routes of travel were chosen to provide the widest possible coverage of the study area. Certain routes were run at frequent intervals, while much of the

[TEXT CONTINUED ON PAGE 48]

19: Talbot E-4,5 (1956-1962)1964 Pl.12 Masai Pl.12

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Figure 7. Check Sheet for Field Personal Observations.

L.M. Talbot
Wildlife Research Project
September 1959

Field Sheet No. Date: Page: Study strip ________ yds.
Purpose: Weather: Area: page ________ sq.mi.
Route: Car Total ________ sq.mi.

Time	Mileage	Veg.	Slope	Erosion	Species	(Group)	♂	♀	?	Remarks

*II C mileage was on compass courses through various types of habitat. Through most of this area there were no roads and no human inhabitants, other than a few nomadic Masai. Most of the country could be traversed at will, except when the grass was high. To ensure sufficient coverage we drove roughly 2,000 miles a month recording the strip. This gave a sample of roughly 200 square miles a month.

*II E Small aircraft (Fig. 8) were used for additional observation and for total counts. After we had established a technique for sex and age class determinations from the air (Talbot and [illegible], 1962) we could get spot population samples from the whole area to check against ground strips. Flights were made at least every other month, usually more often. We also flew strip transects working out the density per square mile, as recommended by [illegible] and [illegible] ([illegible]), to get better basis of comparison between areas. These flights were particularly valuable in determining the timing, location and extent of fires, movements of the Masai and their livestock, and changes in vegetation condition.

19: Talbot E-4,5 (1956-1962)1964 PL.12 Masai PL.12

#12.2
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Figure 6.
A Piper Tri-Pacer aircraft from Wilken Air Services, Nairobi, meeting us on a ridge top landing strip in the study area. We made such strips by driving the Land-Rover back and forth over the area selected. The aircraft flew in from Nairobi as previously arranged. It is a low-speed monoplane with high wings and good visibility, typical of the aircraft so used for aerial survey and census work.

THE PHYSICAL SETTING

The Serengeti-Mara region in Western Masailand is a fan shaped piece of land covering about 20,000 square miles. The wide end of the "fan" lies in the east along the edge of the Great Rift Valley and the narrow point in the west at Lake Victoria (Fig. 1). The eastern edge averages about 6,000 feet elevation with occasional hills and plateaus rising to about 8,000 feet. There is a gentle, irregular slope westward to the lake region at 3,750 feet elevation. The Mau Escarpment and Ngorongoro Highlands rise to over 10,000 feet to the north and south.

Drainage is generally westward into Lake Victoria, the two major exceptions being the Southern Uaso Nyiro River which forms part of the boundary of the region in the north, and which runs south-easterly into the Rift; and the Olduvai Gorge and its watershed which forms an enclosed basin with no outlet at the base of the Ngorongoro Highlands.

Geology

The Great Rift, or Gregory Rift Valley, has been described in detail by *Jaeger* (1911), (1913), Gregory (1921), Willis (1936), and Uhlig and *Jaeger* (1942). The two

*(3) sections of this system that affect the study area are the Eyasi Rift, south and west of the Ngorongoro Highlands, and the main Gregory Rift Valley from Lake Manyara to Lake [illegible] (Fig. 1 and 2). These rifts are basically a result of block faulting along fault lines ([illegible], 1958). The faults are of several ages and faulting activity would appear to have been associated with volcanic activity. The Volcano Lemagrut, at the south-west edge of the Ngorongoro Highlands, is located roughly on the axis of the fault line. Subsequent movement on the fault is diverted through a semicircle on the south side of the volcano and then appears to die away ([illegible], op.cit.). On the east side of the Ngorongoro Highlands, the volcano Oldeani straddles the escarpment and there appear to have been several alternating faultings and eruptions at this point. It appears that both volcanic and tectonic activity in this region started either at the close of the Tertiary or the beginning of the Quaternary and have persisted to present times (ibid.).

The Ngorongoro Highlands, or Crater Highlands, are an uneven plateau at about 8,000 feet elevation, with a series of peaks rising from 2,000 to 4,000 feet higher. Several of the peaks contain craters. The largest crater, the famous Ngorongoro, lies in a low area of the

(3) plateau surrounded by peaks. It is 12 to 15 miles across, roughly 2,000 feet deep, and the floor covers about 100 square miles. Willis (1936) considered it a small rift valley, blocked at the ends. James (op.cit.) considers Ngorongoro and the nearby craters of Embagai and Olomoti to be due to caldera subsidence on a ring fault, with some subsequent in-filling by lake beds. The Highlands are composed of Tertiary volcanic rocks.

In the Rift just northeast of the Ngorongoro Highlands is Mount Lengai, East Africa's only active volcano (Fig. 8). Its conical peak rises to an elevation of 9,443 feet. The volcano occasionally smokes, and periodically it becomes active spewing out large quantities of dust and ashes. Periods of activity may cover several months or longer, the longest continuing from 1915 through 1920 (Guest, 1953). There have been about ten such periods since 1880, or an average of about once each eight years (Guest, op.cit.; Pearsall, 1957). However, since these periods have involved 15 different years, volcanic activity has occurred on an average of one year out of each five and a half during the past 81 years.

The Serengeti Plain is considered to be an

(4a) ancient lake bed. It is largely underlain by rocks of

(TEXT CONTINUED ON PAGE 84)

Figure 8.

Young Masai herd boys at a water hole on the floor of the Rift Valley in Tanganyika. Mt. Lengai, East Africa's only active volcano, is in the background. The view is north with the western wall of the Rift out of the picture to the left.

19: Talbot K-4,5 (1954-1962)1964 Fl.12 Masai Fl.12

*133 134 the Basement Complex, ancient metamorphosed and granitized sedimentary rocks with minor igneous intrusions, all of the Archaean age. Basement Complex is derived largely from shales, sandstones and calcareous sediments. Overlying these rocks are deep deposits of limestones and volcanic ashes, some of which are exposed at Olduvai Gorge (Fig. 10 and 11) where Dr. Leakey has made his famous paleontological discoveries (Hale, 1954; Leakey, 1959).

The surface deposits are calcareous tuff in the east. In the northwestern part of the plains the Basement Complex gives way to granites, which project through in the form of scattered inselbergs or "kopjes." (Fig. 12). Similar kopjes in the eastern plains are of gneiss (Fig. 13).

*135 Much of the northern part of the study area is also underlain by Basement Complex. In the Kenya Mara, a number of separated hills, their summits reaching around 7,000 feet elevation, represent remnants of an end-Cretaceous peneplain. A sub Miocene peneplain underlies parts of the Kenya area, extending discontinuously from the Siria Escarpment eastward through the Loita Hills. This surface is exposed in places, especially on the Siria Escarpment, but further east it is often

(TEXT CONTINUED ON PAGE 59)

19: Talbot E-4,5 (1956-1962)1964 Pl.12 Masai Pl.12

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Figure 56.

Olduvai Gorge, Serengeti Plain, Tanganyika. View to south past exposed Pleistocene water-laid tuffs and other lake beds, the Olduvai Beds in which the artifacts of the Oldowan and Chellean-Acheulian cultures and the "Olduvai Man" have been found.

*133
*,3L

Figure 11.

View southeast across Olduvai Gorge with Mount Lemagrut in the background. Lemagrut, with and elevation of 10,087 feet, is the southernmost volcano in the Ngorongoro Highlands. Note the Bed I-? [illegible] across the gorge.

#13

Figure 13.

Simba Kopjes, eastern Serengeti Plain. Inselbergs of Precambrian granite. Note single acacia tree by largest kopje, remnant of the vegetation cover that surrounded these kopjes before it was cut and burned out by the Masai.

#13

Figure 13.

Kopje on the eastern Serengeti Plain. Inselberg of Precambrian quartzo-felspathic gneiss. Formerly surrounded by woodland; a few isolated Acacias remain.

*133 overlain by Tertiary volcanics.

*133 134 The area near the lower Mara River, leading toward Lake Victoria, is volcanic. Much of the rest of the region south of the Kenya border is granitic, or a mixture of granite, Basement Complex, and quartzites and related rocks of the Ikorongo Series (Bukoba System). Quartzite capped hills and ridges are characteristic of the country from north of the Kenya border south toward the Serengeti Plain, and west to Lake Victoria. These are interspersed with occasional hills capped with Bukoba sandstone or granite, and characteristic granite inselbergs. These similar appearing kopjes are also found occasionally throughout the entire study area.

The area immediately north-west of the Serengeti Plain has a complicated geology. Gold bearing quartz reefs occur in this area, and as a consequence it is particularly well studied geologically (Stockley, 1935; 1936).

Soils

*126 134 Methods: We collected soil samples from most sites of vegetation plots, particularly where it was desireable to examine possible correlations between soils and vegetation, fire, and grazing. We dug over

126 124 100 soil pits in the region of the Serengeti Plain, and collected some material from other areas. The method was as follows: We first dug a pit, about one by two feet or larger, and deep enough to get through the top soil horizon. We then took a soil auger and with it dug a hole a minimum of six feet deep, whenever possible. In some areas rock or particularly hard caliche enforced a shallow pit. In a few cases we took advantage of pits or soft earth and dug down ten or more feet deep. The soil from each auger-full was knocked out in turn along a line to form a long pile with the last auger-full at one end and the first at the other. Samples were then collected from each horizon. A description was written, and the location plotted on our map. The samples were sent to the Scott Agricultural Laboratories in Nairobi, who kindly analyzed them for us. The following discussion is a brief generalized description of the soils of the study area. Detailed results of the soil analyses will be presented where appropriate later in the text.

124 General Description:

/The soils of the Mau and Ngorongoro Highlands are brown or reddish, silty loams derived from volcanic ash. These are underlain by clay or clay loam which is often exposed by erosion. Under forest conditions the humus content of the top soil is high, but erosion is relatively swift when the vegetation is

139 cleared by fire, cutting, or grazing.

The eastern Serengeti Plain has a soil derived
from, and often largely composed of, calcareous tuff.
It is a medium to fine-grained grey-brown tuff which
covers the whole of the eastern plains and many of the
*133 surrounding hill tops. The Salei Plain and adjacent
139 parts of the Serengeti Plain are covered by dunes of
black volcanic ash. The ash comes from the periodic
volcanic activity of Lengai volcano which is immediately
*{131} to the southeast. Southeast winds prevail most of the
year, and although the dunes are mostly stabilized
by vegetation (Fig. 14), the influence of the winds can
be clearly seen in their form and orientation. At
several points in the eastern Serengeti there are small
shifting dunes, famous in East Africa as the "Shifting
Sands." These are actually small unstabilized barchans
formed of the same black ash. In periods of volcanic
activity considerable quantities of this ash are
deposited over the plains. Residents of Tanganyika told
us of travelling through the central plains immediately
after an eruption and of finding ash covering everything
in deposits up to two feet thick at distances of some
139 40 miles from the volcano. These eastern soils are
immature, often undifferentiated to a considerable
depth. The texture is very loose. Except where

(TEXT CONTINUED ON PAGE 63)

19: Talbot K-4.3 (1956-1962)1964 PL.12 Mosaic PL.12

#19

Figure 19.

Southeastern Serengeti Plain. The soil is blown volcanic ash from Mount Lengai, stabilized by vegetation. The hill in the background is Precambrian quartzite. Note the hummock effect where loose ash has been blown from between the clumps of grass and forbs. Wildebeeste and zebra in background.

(19 stabilized by a good vegetation cover, the soil surface and the organic matter are frequently in motion, being blown eastward. These soils are quite rich in soluble minerals but very low in nitrogen, especially where vegetation cover is lacking. They often have a shallow underlying hardpan (Fig. 13).

To the west of the Serengeti Plain the loose ash grades into gray and black sedimentary soils. In the lower, less well drained areas these soils are heavy calcareous black or gray clays, the [illegible] "Black Cotton" clay of East Africa. Underlying these surface loams or clays is often a red clay, and to the north and west of the Serengeti Plain, except in the valley bottoms, the predominant surface soils are red earths. Heavy black loam or clays are found in the valley bottoms, especially in the valleys of the Grumeti and Mbalangeti Rivers. There is a clearly defined catena structure on the slopes of the western hills, extending from the exposed rocks on the ridge tops through the red earth slopes to the dark sedimentary soils in the bottoms.

North to the Kenya border the red earths predominate, with black heavy sediments in the bottoms and catena structures similar to those of the western

(TEXT CONTINUED ON PAGE 65)

19: Talbot E-4,5 (1956-1962)1964 Pl.12 Masai Pl.12

Figure 19.

Southern Serengeti Plain. Hardpan exposed by erosion due to overgrazing. Soil is derived from tuff and volcanic ash.

(2% area. The valley of the Mara River in Tanganyika has soils derived from volcanic material. In the Kenya Mara the progression of soil types from west to east is similar to that in the Serengeti. In the Mara Plains the bottoms are typically heavy gray or black loam or clay. This grades to red soils on the surrounding hills, and to a light, calcareous soil derived from volcanic ash on the Loita Plain in the east.

Climate

6% 12.6 122 Because of the isolation of the area and the low human population, climatic data from Western Masailand are very sketchy. However, there are some data from records of the East African Meteorological Department at Nairobi, the District Administration at Narok, and the Serengeti National Park. The following discussion is based on these records and our own observations.

121 Western Masailand lies within the Tropical Savanna (Aw) Climate. Local factors influencing the weather in this area include the mountain masses bordering the area to the north and south, Lake Victoria to the west, and the arid Rift to the east (Fig. 8).

131. Rainfall: Rainfall is relatively high in the neighborhood of Lake Victoria and becomes less toward the east. The gradient in average annual rainfall is from around 40 inches in the west to about 20 inches near the Rift. Near Lake Victoria there is significant rainfall throughout the year and dry periods are relatively short. Throughout most of the rest of the study area there are significant dry periods, and rainfall is considered to fall in two periods, the "long rains" of March through May, and the "short rains" of November and December. However, examination of the records show that throughout the study area there appears to be one long but discontinuous rainy season extending from November through May, with peaks in March and April, and sometimes a decline in rainfall in January. [21] Possibly the reason for the widespread belief in two distinct rainy seasons, even on the part of residents in the area, is the nature of the rains. During the peak of the traditional long rains, in March and April, the cloud cover is general at least during the afternoons, when it amounts to a high overcast. For most of the rest of the year rainfall comes from less general storms or showers which pass quickly, or occasional general but brief storms. In the traditional short rains the overcast and rains are more widespread. During the period between the rains, late December

(13) through February, the average monthly rainfall may remain about the same as December, but the storms are brief and not accompanied by long lasting, widespread overcast. The less sun there is, the less is the evaporation, (see below) so during the traditional "short rains" the ground surface may be moist longer than during the following period.

The distribution and reliability of the rainfall is of far greater ecological importance than the total amounts of precipitation. The rainfall in Western Masai-land is highly irregular in both occurrence and distribution. Much of the area is likely to receive less than 20 inches of rain in about one year out of four (Glover and Robinson, 1953). Rain may fall during any month of the year, but except during the peak of the "long rains" the rain is in the form of localized storms (Fig 10) and many areas are missed completely. Seen from an airplane in any month other than late March and April the country usually has a mottled appearance, with the locations of recent rainfall marked by scattered green spots and strips on the dry brown or burned black background. Tables 1, 2, and 3 show the monthly variation in rainfall from five stations in the Serengeti region. For their locations see Fig. 3.[A] They illustrate well the extreme irregularity of precipitation on the study area.

[A] [See p. 13.--Analyst]

*/25
*/22

Figure 19.

Isolated rain storms in Ngorongoro Crater. This rainfall is typical of the dry season precipitation in Eastern Maasailand. The shower on the left is mostly evaporated before it reaches the ground. The storm on the right is torrential causing heavy run-off. Both are very localised and the ground around them remains dry. The light coloured deposits are alkali from the dry lake bed in Ngorongoro.

Table 1. Summary of Records from [illegible] and [illegible] Illustrating the Irregularity of Rainfall in the [illegible] Part of [illegible]

[illegible]

[illegible]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Max.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Min.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Rainfall days	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Yearly rainfall [illegible]

[illegible]

[illegible]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Max.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Min.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Rainfall days	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Yearly rainfall [illegible]

[illegible]

Table [illegible]. [illegible]

[illegible]

[illegible]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Max.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Min.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Rainfall days	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

[illegible]

[illegible]

[illegible]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Max.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Min.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Rainfall days	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

[illegible]

[illegible]

Table [illegible]

[illegible]

[illegible]

[illegible]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Max.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Min.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

[illegible]

[illegible]

[illegible]

133. Outside of the peak rainfall, most precipitation comes in the form of torrential storms or brief, light showers. The maximum amount of rain recorded in any 24 hour period in the study area is only 3.5 inches, but many storms only last a few minutes. The rainfall may be so heavy in these scattered storms that where they pass over areas without a high vegetation cover, the splash creates a ground-obscuring mist two to three feet high. We measured up to 0.45 inches of precipitation from such storms, which often lasted less than a half hour.

[134] There is very heavy run-off following such storms and unless there is a good vegetation cover the combination of the splash impact and the run-off causes considerable erosion.

The light showers frequently do not even reach the ground, and when they do they often have relatively little effect. The ground surface is hot and a desiccating wind usually blows day and night. Much of the precipitation that reaches the ground from light showers is evaporated almost before the cloud passes on.

During the peak of the rains the daily precipitation is somewhat higher than the yearly average (Table 4). Due to the more general overcast there is less evaporation

[TEXT CONTINUED ON PAGE 74]

*132

Table 4. Summary of Rainfall Records at Banagi, Tanganyika, for the Period 1938 through 1959.

Month	Mean Days of Rain	Mean Inches Rain per Day of Rain	Mean Total Inches Rain for Month	Per Cent of Years with Below Mean Rainfall in Month	Number of Years with No Rain in Month
January	9.0	0.33	2.950	50	1
February	8.2	0.39	3.225	55	0
March	9.9	0.48	4.770	59	0
April	10.8	0.45	4.895	50	0
May	8.4	0.34	2.831	59	0
June	4.7	0.28	1.301	50	2
July	2.6	0.41	1.062	73	3
August	4.9	0.32	1.583	55	1
September	4.7	0.24	1.125	50	3
October	3.5	0.35	1.216	59	1
November	6.6	0.33	2.149	68	0
December	9.2	0.38	3.461	64	1
Average by month on a yearlong basis:	6.9	0.36	2.548	57.7	
Average of year (Range)	82.3 (37-109)		30.42 (18.44-42.24)(1)		

(1) Number of years with below average rainfall: 14 (63.6 per cent).

*132 and the rain that falls in that period is more effective in terms of plant use and augmenting sub-surface waters than equivalent amounts of rainfall at other seasons.

Table 4 summarizes the rainfall records over a 22 year period at Banagi. This is the most centrally located weather station from which records are available covering a relatively long period. Banagi lies at just below 5,000 feet elevation, a few miles north of the northern edge of the Serengeti Plain (Fig. 3).[1] Although the actual amounts of precipitation, and to some extent, the pattern of rainfall vary through the study area, some general inferences may be drawn from the Banagi rainfall data that appear valid for most of the plains region.

About a third of the average annual rainfall comes during the two wettest months, March and April. Even in these months rain is only expected about every third day on any given point, although there is usually rain somewhere in the region every day. During the five months, June through October, about a fifth of the annual precipitation is received, but it comes in very scattered showers which occur on the average of about four days a month. Starting in November the monthly precipitation increases gradually to a peak in April. The number of days per month with rain remains relatively constant at

[1] [See p. 19.--Analyst]

*132 about nine between December and May, but the amount of rain received per day with rain increases from November to March and April, then tails off. Average daily rainfall and total rainfall drop slightly in January.

Based on the 22 years of record, there is a greater than 50 per cent probability of receiving below average rainfall in eight months of the year. Below average annual rainfall can be expected in two years out of three. The only months in which rainfall has not failed completely in at least one year are February through May and November. In November, however, in about a quarter of the years the total monthly rainfall was on the order of 0.2 inches or less, and in the months February through May there are years with a monthly total of about one inch or less for each month.

Temperature, _Humidity_, _and_ _Evaporation_: The study area is located roughly between 1°00' and 3°40' south latitude. The temperatures in the area are highest in the period of the Northern Hemisphere's winter, and lowest in the northern summer.

Table 5 summarizes the temperature data from in and around the study area. There are very few recording stations in the study area. However, from the available

[TEXT CONTINUED ON PAGE 77]

Table 5. Summary of Yearlong Temperature Records from Study Area

	West Edge(1) (Musoma, on (Lake Victoria)	Northwest Edge(1) (Lolgorian)	Center(2)	North Edge(1) (Narok)	Outside East Edge(1) (Rift Floor)
Years of Record:	10	2	2	21	21
Elevation in Feet:	3762	5500	5000-6000	6200	2010
Absolute Maximum:	95		100	87.5	107.2
Mean Maximum:	83	85.8	86.9	79.9	98.7
Mean:	74.1	69.6		61.7	84.4
Mean Minimum:	65	58.5	56.5	45.9	74.8
Absolute Minimum:	52.5		51	32.5	66.0
Mean Diurnal Range:		24.3	30.7	28.9	21.0

(1) Data from East African Meteorological Department.

(2) Data from this study.

*132 data and knowledge of the elevations of the study area it is possible to calculate temperatures. The East African meteorological Department (1959) has shown that there is a close statistical correlation between height and mean maximum and minimum temperature. The correlation is high enough that if the height of a location is known its temperature may be calculated with a probable error *125 of only some 2° F. (Ibid.). The Meteorological *132 Department publication gives a series of formulae for calculating mean, maximum and minimum temperatures on a monthly or annual basis. These formulae are based on the calculation of a 3.56° F. drop in mean annual temperature for each 1,000 feet rise above sea level, with equivalent drops of 3.26° in maximum temperature and 3.86° in minimum temperature. The formula given for mean annual temperature is: 86.3 - 3.56 x (where x = height in 1,000's of feet). Applying this formula to several of the stations listed in Table 5 gives the results shown in Table 6.

Most of the study area lies at an elevation of 5,000 to 6,000 feet. Using the above calculation, the mean annual temperatures over this area would be around 64.9° to 68.5° F., with a probable error of about 2°. The formula given for mean maximum annual temperature is 96.0 - 3.26x ; and that for mean minimum annual

*132

Table 6. Comparison of Calculated and Recorded Mean Annual Temperatures.

	Musoma	Lolgorian	Narok
Elevation (feet above sea level):	3762	5500	6200
Calculated mean annual temperature (degrees Fahrenheit):	72.91	66.72	64.23
Recorded mean annual temperature (degrees Fahrenheit):	74.1	69.6	61.7
Error:	-1.19	-2.88	+2.53

*125 *132 temperature is 76.6 - 3.86x (Ibid.). Using these formulae for the part of the study area at 5,000 to 6,000 feet elevation, the mean minimum temperatures should range from about 53.4° to 57.3°, and the mean maximum 76.4° to 79.7°. The figures we obtained (Table 5) show a somewhat wider temperature range. This may be due to the method of measurement of temperature. The Meteorological Department measures temperature with a standard maximum-minimum or recording thermometer in a standard meteorological screen. Our temperatures were taken with a standard maximum-minimum thermometer situated about five feet above the ground surface, in the shade wherever we happened to be. Thus our readings are an average of air temperatures in the shade throughout the area rather than those in a standardized screen in one spot.

*132 At Narok, at the northern edge of the area, on the basis of mean monthly temperatures July (58.6° .) and August (59.2°F.) are the coldest months, and March (63.6° F.) and April (63.8° F.) are the hottest. On the basis of mean minimum monthly temperatures, September (45.0° F.) and October (45.4° F.) are coldest. The highest mean maximum monthly temperatures are in February (80.6° F.) and January (79.9° F.). The range between the mean temperatures of the hottest and coldest months is 5.2° F.

*132 Near Lake Victoria September, October and November are the hottest months and June, July, and August the coldest. The daily and seasonal ranges in temperature are narrow, presumably because of the influence of the lake. The range between the mean monthly temperature of the hottest month (76.1° F.) and the coldest (72.5° F.) is 3.6° F.

The hottest temperatures recorded in or near the study area come from the floor of the Rift. There February and March have the highest mean monthly temperatures (87.6° F. and 87.3° F.), and June and July the lowest (81.0° F. and 80.5° F.).

In the center of the area November through February are the hottest months and June, July and August the coldest. The diurnal range in temperatures is greatest in the hot season. The maximum range that we recorded was 42° F. in November, and the minimum diurnal range was 21° F., in June and July.

The mean maximum was lowest in June and July (80.6° F.) and highest in November and January (91.4° F. and 92.0° F.), and the mean minimum was also lowest in June and July (55.0° F.) and highest in December and January (57.5° F. and 57.3° F.). The absolute maximum

*132 temperatures were recorded in January.

Temperature ranges are greater on the open plains than in wooded country, and the highest absolute air temperatures are over areas of bare or nearly bare ground. Rainfall swiftly reduces air temperature by 10 to 15 degrees F. This is illustrated by the temperatures recorded during a short storm in November, 1960. At 1330 there were scattered cumulous clouds but it was generally sunny and the temperature was 86° F. A sudden sharp rain started. Table 7 summarizes the temperature changes.

This storm lasted about 80 minutes, with rain actually falling for less than an hour. Rainfall was about 0.2". The storm was widespread enough that even after the storm passed us the wind remained cool for a time. During the first ten minutes there was a temperature drop of almost one degree a minute. After the first sun it required about 45 minutes for the air temperature to return to normal. In the usual 15 to 30 minute storms of the dry season there is a rapid 10 to 15 degree drop in air temperature, which then returns to normal 10 to 20 minutes after sunlight returns. Thus the rain storms are of great significance in the temperature regime and therefore, the evaporation,

[TEXT CONTINUED ON PAGE 83]

*132 Table 7. Changes in Air Temperature Caused by a Rain Storm, November, 1960.

Time, Minutes from Start of Storm	Air Temperature Degrees F.	Conditions
- 1	86	Sunny with scattered cumulous clouds.
1	85	Heavy rain.
3	84	Heavy rain.
5	83	Heavy rain.
6	82	
7	80	Rain slacking.
9	78	
14	77	Rain tailing off. Ground still warm, rocks warm and dry.
22	76	Rain starting again.
27	74	
33	70	Rain tailing off.
37	68	Rain over, wind cool and moist.
50	67	
55	67 1/2	
59	68	Sprinkling.
64	69	
80	71	First sun, but scattered clouds.
100	74	
110	78	
125	82	Normal temperature for this time of day.

*132 of the area. The brief storms that bring most of the annual rainfall do not lower temperature long enough to much reduce the evaporation, hence little of this rain may be effective. Only during the more generalized storms of March, April and sometimes late November or December is the rainfall and cloud cover general enough to much reduce evaporation. Since these are the hot months, however, the evaporation is still relatively high.

The air temperature is lowest between 0400 and 0600 hours. It rises suddenly when the sun first appears, about 0630 the year round, then climbs more slowly until about 1100. The temperature peaks are between 1300 and 1600, and after 1700 it drops fairly steeply until 2000, then drops gently until 0400.

The relative humidity describes a diurnal curve that is the mirror image of the temperature curve. During the cool months the high point before dawn may be around 70 to 80 per cent relative humidity, which drops rapidly to around 20 percent by mid-afternoon. The mean diurnal range of relative humidity at Narok averages 58 per cent. . The maximum ranges occur in October (67%) , January (68%) and February (70%) and the minimum in May and June (44% and 47%). The mean relative humidity is highest in the cold months of

*132 of April through July.

Table 7[1] notes that even after about 15 minutes of rain, half of it quite heavy, the ground was still warm and the rocks dry. This entry illustrates the high evaporation which is characteristic of the study area. There are several methods for estimating the evaporation or potential evaporation of the area. On the basis of ten years' readings from a Piche Evaporimeter, the mean evaporation at Narok is estimated at 0.23 inches a day, or 84.79 inches a year. By an Evaporation Pan in use two years the annual evaporation at Narok was estimated to be 61.95 inches. Using Thornthwaite's method calculated for East Africa the potential evaporation at Narok would be in the order of 34 inches. In any case, the evaporation is very high and [illegible] exceeds
*125 the rainfall. By Thornthwaite's method, an elevation
*132 of about 7,000 feet would have to be reached in the study area before the rainfall exceeded the potential evaporation (Pearsall, 1957). By the same method the potential evaporation for most of the study area would range up to about 40 inches. Based on a water consultant's report and other information, the potential evaporation rate for much of the study area must be at least on the order of 50-60 inches per year (Pearsall, 1957).

[1] [See p. 82--Analyst]

*132 Wind: The prevailing wind throughout the year in much of the study area is southeast, occasionally south or east. Average winds appear to be a little above five miles per hour, although winds of up to 22 knots (25.3 m.p.h.) have been recorded in every month at Narok. On the eastern plains the normal winds appear to be Moderate to Fresh Breezes (13 - 24 m.p.h.) according to the specifications for the Beaufort scale of wind force (Kendall, et. al., 1951:78). By the same criteria, strong breezes (25-31 m.p.h.) and moderate gales (32-38 m.p.h.) occasionally occur throughout the area. At ground level winds are stronger and more constant in the east than in the west. They appear higher on the northern Loita Plain than farther south. Wind effect is greater on high ground than low, and on open land than under trees or brush.

Storms: Hail storms occurred several times in the northern part of the study area, near the Mau Escarpment. We never saw hail in the central plains.

One evening, nearly at dusk, during the heavy rains which produced floods in November, 1961, we saw a tall, thin, columnar cyclone moving northwestward across the Serengeti Plain. It apparently extended over 2,000 feet into the air, ending in a small cloud somewhat

*122 below the general overcast. We watched it at a range of about 10 miles for about 15 minutes, before it passed out of sight. Small "dust devils" were common on any hot, windy day, but this was the only large scale cyclonic column of this sort that we saw. Roosevelt (1910) referred to seeing "a waterspout or cyclone" one stormy evening near Mt. Kenya. This is the only other reference we have found to this phenomena.

Summary: Western Masailand lies within the Tropical Savanna (Aw) Climate, and local weather influences include the Lake Victoria on the west, mountain masses in the north and south, and the arid Rift Valley on the east. Average annual rainfall follows a gradient from about 40 inches near Lake Victoria to about 20 near the Rift. Some rain may fall in any month, but the most rainy period is November through May, with peaks in March and April. Rainfall is very irregular in occurrence and distribution; two years out of three expect below average rainfall, and one year out of four expects less [134] than 20 inches. Most rain falls in the form of short torrential storms or showers, hence much of the rainfall may be lost to the vegetation and underground water supplies through immediate erosive run-off or evaporation. Potential evaporation appears to exceed

*132 rainfall at all elevations below 7,000 feet. Mean annual temperatures are between about 61 and 74 degrees F., with mean maximum temperatures of about 76 to 87 degrees, and mean minimum temperatures of about 46 to 65 degrees. In the center of the area the coldest months are June and July, and the hottest November through February. The diurnal temperature range is greatest in the hot months, reaching a maximum of 42 degrees.

From the standpoint of ecology, the climate of the study area can be characterized as having moderate to high temperatures; low, irregular and poorly distributed precipitation; seasonal droughts; and high evaporation.

Water Supplies

*133 The main catchment areas for Western Masailand are the Mau Escarpment, the Loita Plateau, and the hill system extending south and west of it. The Mara and Guaso Nyiro Rivers are the two largest perennial waters in the north rising on the Mau. The Grumeti, Mbalangeti, and Duma rivers are the most significant rivers in the south. Of these major watercourses the Guaso Nyiro is largely outside the study area and only the Mara maintains a significant flow during drought periods. The southern rivers all tend to cease running in dry periods but they leave occasional pools which are of great importance to the wildlife (Fig. 17).

*13

Figure 17.

Dry season pools in an intermittent river north of the Serengeti Plain. When these watercourses stop flowing occasional pools are left. Some persist throughout most dry seasons, others dry within a few weeks. These pools provide most of the dry season water for the wild animals of Western Masailand.

*133 The map (Fig. 3)[i] shows the numbers of rivers that rise in the hills from the Kenya border to the northern edge of the Serengeti Plain. The Bologonja and several smaller springs are perennial, but most of these watercourses flow only during wet periods, or following occasional heavy rains during the dry periods (Fig. 18). At this time the catchment areas of the scattered hills are critically important.

*13 In the hills between the boundary of the Serengeti National Park and Loliondo, cutting, overburning, and overgrazing by the Masai have seriously reduced the watershed values of the area. Runoff is torrential after rains, and virtually no dry season surface water
[312] is available through the area. There are several
*[237] bore holes (Fig. 19) which have the effect of concentrating livestock and causing very severe overgrazing in the vicinity.

[164] Across the hills in the park destruction of the vegetation has been very much less, largely because it is an area infested by tsetse fly, so the Masai have not grazed it much. The vegetation provides fair watershed and even the scattered dry season storms produce some surface water.

[i] [See p. 19.--Analyst]

*133

Figure 18.

Lower Olduvai Gorge, an example of an intermittent stream flowing immediately following a rain.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

*133
512
379
$233

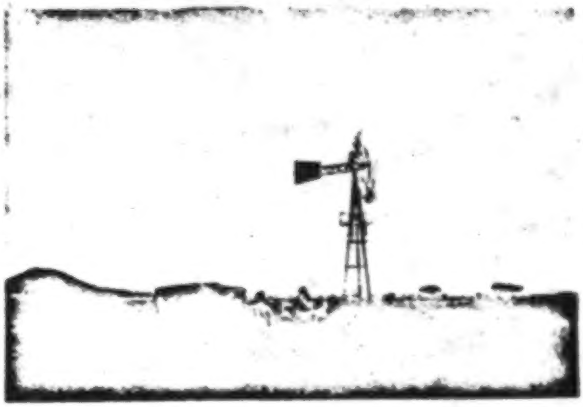

Figure 19.

Bore hole with windmill in north-eastern Serengeti Plain. This was put in to provide dry season water for the Masai livestock. When the picture was taken (1956) the well was not in operation, consequently there was some grass cover remaining.

312 In the open Serengeti Plain there are a few springs and wells. The high evaporation tends to concentrate any stored water in the plains region and as a result the water supplies are limited and they are mostly saline or alkaline. Pearsall (1957) has presented a series of tables showing the analysis of water samples from the water sources of the Serengeti region.

*13 During the long rains low spots collect standing water throughout the plains of the study area (Fig. 20). Particularly on the eastern areas there is an impermeable hard pan near the surface (Fig. 15),[1] and much precipitation remains on the surface in low spots until it evaporates or is drunk by the animals. The longer the water stands, the more saline or alkaline it becomes through evaporation.

[1] [See p. 64.--Analyst]

The Ngorongoro Highlands provide a large catchment area principally for the area to the south, outside of the study area. There are a few streams and springs on the north-western flanks of the mountains that are of importance for wildlife and domestic livestock.

Throughout the study area, wherever watersheds are accessible to the Masai they are damaged. In the north, through burning and overgrazing the watersheds of the Mau Escarpment and the Loita Plateau are being

[TEXT CONTINUED ON PAGE 94]

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Figure 20.

Rain pools on the western Serengeti Plain. At the start of the long dry season some water remains in such pools for periods up to two or three weeks. This water enables some wildlife to continue grazing on the plains until the water is exhausted, evaporated, or becomes too alkaline or saline. Kongonis, Grant's gazelles, and zebras are drinking.

*13 seriously damaged (Darling, 1960; Talbot, 1960c). The same is true for the Ngorongoro Highlands (Pearsall, 1957; Pereira, 1960).

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312 Summary: Permanent waters exist in Western Masailand in the form of a few rivers, springs, and wells. Seasonal water comes from standing rainwater in the open plains during the wet seasons, and pools of water in the bush country watercourses during the dry season. Watersheds on the Mau Escarpment, the Ngorongoro Highlands, Loita Plateau and numerous small hills are of critical importance to provide dry season water. Wherever they are accessible to Masai livestock the catchment areas are overgrazed, and normally overburned.

THE MASAI

Introduction

121 *13 The Masai have been a key factor in the isolation and hence, survival of the primitive grassland ecosystem of Western Masailand. Through their fires and livestock they are also one of the principal components of the *114 ecosystem. Although there are extensive writings on the Masai there have been very few intensive studies. Most writings are the observations of government officers assigned to Masailand or of missionaries. The general outline of Masai history appears fairly well known, but we found many conflicting ideas and surprisingly little precise information on these interesting people at present. Visiting anthropologists and socialogists have given us detailed and dogmatic descriptions of Masai land use and ways of life. These descriptions often conflicted with one another and often were totally at variance with the conditions we had observed living near the Masai for over two years. It appears to us that there are two basic reasons for this situation:

*114 181 In the first place, most people who deal with the Masai become strongly partisan about them. There is something of the Lawrencesque "Noble Bedouin" charm about the Masai. They were and are warriors (Fig. 21)

[TEXT CONTINUED ON PAGE 97]

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Figure 21.

A Masai junior elder from Tanganyika. He has served his period as a warrior, then at the olngesherr ceremony he shaved off his pigtail hair-do and became a junior elder. The facial scarification marks him as belonging to one of the fringe sub-sections of the Masai tribe.

*114 181 and within the century they ruled most of East Africa. To a large degree they have maintained their own free way of life and they haughtily refuse to accept the *114 123 clothes and other trappings of western life. To people coming from crowded and regimented countries there is a much to admire and envy in the Masai. In its more extreme forms this admiration is known in East Africa as Masai-itis.

*114 *13 181 On the other hand, some administrators who must deal with the Masai find frustrating at best their often-complete mistrust and rejection of foreign ideas. Most of those concerned with land use and managment of East Africa's natural resources see the Masai, like the Arab, as the father of the desert and not its son. [123] The strong feelings between those with "Masai-itis" and those with "anti-Masai-itis" are sometimes reflected in their reports and publications.

*114 184 The other factor contributing to confusion about the Masai is the general tendency to regard them as one unified group. Actually there are a number of separate sections of the Masai, some of them pastoral, some agricultural, and some in-between. There are very significant differences in customs involving land use even between adjoining groups of pastoral Masai.

114 184 Consequently one must specify which Masai he is speaking of, where, and when; it is not valid to generalize about "the Masai."

History

121 Man is the ecological dominant, therefore knowledge of human history of an area is basic to understanding of its ecological history. For this reason I have gone into the history of the Masai in some detail.

174 Before 1800: The early history of the Masai has been discussed by a number of writers. Among the important works are those by Fosbrooke (1948, 1956), Gower (1948), Grant (1954, 1957), Hollis (1905), Leakey (1930), Peters (1891), Sanford (1919), Simon (1962), and Thomson (1885). The following summary is drawn from these writings.

[144] The Masai are considered to be of Nilo-Hamitic stock. It is believed that about 400 years ago they occupied a lowland country north and west of Lake Rudolph in northern Kenya. According to their own traditions they (subsequently) occupied a country called Kieru which must have been the Rift Valley between Lake Rudolph and the Kenya Highlands. This area lies about

174 160-200 miles airline north of Western Masailand, and
174 it is a desert at present. A tribal elder called
173 Maasinda found a way to climb the escarpment at the south
of Kieru and some of the tribe then moved into the Kenya
[614] Highlands. The legendary Maasinda had six sons who
became the founders of the present six Masai clans.

The tribe gradually moved south. At Ngong, near Nairobi, according to their traditions they found a Heaven-born child who became their first Laibon
174 or Medicine Man (Hollis, 1905). Fosbrooke (1948) dated the arrival at Ngong at 1640 on the basis of the geneology of the Laibons founded by that legendary first child. During the next 150 years the Masai moved over 300 miles airline southward.

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175 1800-1890: By 1800 a few Masai had made what proved to be the tribe's maximum penetration into Tanganyika but it was not until about 1880 that they had completed their occupation of what is now the Masai Steppe in Tanganyika (Fig. 1).[1] There had been constant warfare and raiding involved in this settlement, and the margins of Masailand fluctuated somewhat. For a time the Masai occupied the area immediately south of the Ngorongoro Highlands, as well as lands near Mt. Kilimanjaro and Mt. Meru that are now in other hands.

[1] [See p. 9a.--Analyst]

175 177 The people whom the Masai displaced in Tanganyika were mostly pastoralists. There were also some small tribes who practiced irrigated cultivation near the Rift wall and on some mountain flanks. Those who immediately preceeded the present Masai may have been related to them, and they, in turn, evicted prior residents. Some of these early people dug wells and built dams, but Fosbrooke (1948) believes that except for irrigation systems on some mountains, these waterworks were for pastoralism rather than agriculture. There were also isolated tribes of metal workers in the south who may have provided the Masai with spears and knives.

175 [131] In the study area, the Masai occupation of the Ngorongoro Highlands and the Serengeti Plain was probably
175 648 completed by 1850. A people called the Il Datwa occupied the highlands and much of the rest of the area, both north and south of Ngorongoro. These were probably both pastoralists and cultivators. Another similar tribe, the Sonjo, lived near the foot of the Rift near Lake Natron.

Somewhere between 1836 and 1851 the Masai drove the Il Datwa off of the Crater Highlands and the Serengeti Plain. The limestone wells of the eastern

175 [648] Serengeti are said by the Masai to have been dug by the Il Datwa, and they still call the Ngorongoro Highlands "Osopago lol Datwa" in memory of the people from whom
175 131 they took the area. In the next 15 years the Masai took the flat land immediately south of the highlands. Then, until about 1890, several section and sub sections of the Masai occupied the entire Serengeti Plain, the Ngorongoro Highlands, and the lands immediately west of the Rift. They lost the land south of the highlands through incursion of the tsetse fly, just as they lost other lands to the east and south of the present Masailand.

During the period of 1860 to 1890 the Masai were a prosperous tribe and they probably reached their maximum land holdings and cattle numbers. The area they occupied extended roughly 500 miles from north to south and 150 miles from east to west, an estimated
175 721 80,000 square miles. Under the leadership of their paramount Laibon, Mbatian, they raided from Lake Victoria to the Indian Ocean. Sanford (1919) and Simon (1962) quote excerpts from the writings of many early explorers referring to the extent and effect of these Masai raids. The raids were not confined to other tribes, however. Some of their more devestating battles took place between different sections of the Masai themselves.

175 1890-1900: About 1890, at the peak of their
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*233 power and prosperity, the Masai were stricken by famine, smallpox, and rinderpest. The effects of a protracted drought about 1890 were intensified by rinderpest. This infectious virus disease is often fatal to cattle and many wild ungulates. It was introduced into Abyssinia and Egypt from India and the Black Sea in the late 1880's (Percival, 1928). By 1896 it had swept into South Africa, killing many of Africa's domestic and wild ungulates on the way. The disease entered Masailand in 1891 via some diseased cattle stolen by the Masai at Loitokitok (Percival, op. cit.). At nearly the same time it may have entered Masailand in the north and south west. It rapidly spread to virtually all the cattle of the Masai, as well as to many of the wild animals. At the same time a smallpox epidemic struck the Masai. Baumann (1894), who entered the Ngorongoro Crater in 1891, wrote a graphic account of the pitiful condition of the sick and dying Masai he encountered on the Crater floor.

As a result of these multiple disasters, many areas formerly occupied by the tribe were emptied, the cattle gone, and the people dead or scattered.

175 During the famine, the Laibon Mbatian died. His

175 two sons, Lenana and Sendeyo, both vied for his position. About 1896 open civil war broke out. Sendeyo was backed by the Loita Section of the Masai, from the Loita Plateau area, while Lenana was primarily supported by the Purko Section from Kenya. The Loita attacked the other Masai moving north and east to Nairobi before they turned back. They then returned and defeated the sections of Masai who had occupied the Salei Plain (Fig. 3), the Serengeti, and the Ngorongoro Highlands. Sendeyo made his headquarters near Ngorongoro Crater.

For a time Sendeyo's forces appeared paramount. They raided down across the rift valley and had a number of skirmishes with the Germans as well as the other sections of Masai. Finally the Purko joined forces with the Kissongo, a large section mostly from Tanganyika's Eastern Masailand. The two forces made a clever and successful flank attack on Sendeyo. The Kissongo attacked from the east while the Purko came from the north via Loliondo. When they converged on Sendeyo in the Ngorongoro Highlands he surrendered. Part of his warriors met a spectacular death in the Embagai Crater when a Kissongo war party forced them over the high rock cliff in the south east wall.

European Period: By 1902 the civil war was over

175 but so was the absolute reign of the Masai. The organiza-
175 tion of the sections was much broken up. Many pastoral
*233 Masai had lost their herds and had taken to hunting or
cultivation. Some had been taken in by surrounding
tribes and others taken as captives by them. A great
many had died or been killed in the combination of famine,
[161] rinderpest, smallpox, and civil war. Therefore the
population of Masai in Masailand around 1900 must have
been quite low. Its lowest ebb probably came around
1892 or 1893, and there had been some recovery in the
next decade. Some Masai had started to rebuild their
[648] herds by stealing cattle. Others bought them by
[721] working for the Germans helping to subdue other tribes.

175 It is uncertain what the fate of the Masai would
648 have been without the intervention of the Europeans.
Those most afflicted with Masai-itis insist that the Masai were recovering rapidly and that they would have risen to greater power but for the Europeans, who held them down and took their land. Those on the other side say that the Masai were a dying race and that only the protection of the Europeans enabled them to maintain their way of life. The truth doubtless lies between the extreme views. Even Hollis (1905) who was certainly not anti-Masai felt that they would have to alter their way of life if they were to survive.

175 161 In terms of total population the Masai have greatly prospered under European administration. It has been estimated that at the peak of Masai power, before 1890, the total population of Masai was around 45,000 (Simon, 1962). By the mid 1920's they had recovered from their series of disasters and their numbers were estimated at about 50,000 (Joelson, 1928). The census of 1948 gave the total Masai population as 107,309 (Fosbrooke, 1948). The most recent census places the population at about 117,000.

175 648 Most of the Masai prosperity in the 20th century has taken place under the English administration. In 1891 the boundaries of the German Territory of Tanganyika stopped short of what is now Tanganyika Masailand, but it was included in the German "sphere of interest." [657] (Kiepert, 1891). Subsequently, apparently because there were so few Masai living in Masailand following their multiple disasters, the Germans created a Masai Reserve that was mostly south of an east-west line through Arusha. This division left the Ngorongoro Highlands, the Loliondo area, and the highlands near Eastern Masailand free for European settlement and displaced the Masai living there. [131] This action further scattered the remnants of the Masai, some of whom moved north into Kenya and others south into

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131 the German Masai Reserve. After the 1914-18 war the English allowed the Masai to return to most of the areas they formerly occupied in Tanganyika.

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648 After defeating his brother, Lenana returned to Kenya and in 1902 he peacefully acknowledged British rule. The Masai were still very few in numbers but they ranged over a wide area of Kenya, grazing their cattle
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131 and raiding. In 1904 two Masai reserves were created, a northern one of some 4,500 square miles in the Laikipia area, northeast of Western Masailand, and a southern one of about 4,350 square miles which included part of the present Eastern Masailand in Kenya. The Masai, led by Lenana, signed a treaty accepting the reserves in August 1904. This arrangement did not prove satisfactory for either the Masai or the English. Lenana found it difficult to control the northern Masai when he was in the south and requested that the reserved be joined. Consequently, after several years of negotiations, a treaty was signed in 1911 in which the Masai gave up the 4,500 square miles of the Northern Reserve and received in return over 9,000 square miles of land including what is now the Kenya portion of Western Masailand. Part of this area was unoccupied, some of it was European ranch land, and part of it had been occupied in former times by Masai. This new half of the Southern

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648 Reserve became Narok District, with headquarters at
667 Narok. The remainder of the Southern Reserve was
131 Kajiado District, with its headquarters at Kajiado, about 45 miles south of Nairobi on the Great North Road (Fig. 1). The Provincial headquarters for both districts was located at Ngong, just west of Nairobi.

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131 With subsequent extensions, the Masai in Kenya received a total of over 15,000 square miles which included some of the finest grazing and forest land in Kenya.

Partisans of the Masai say that the treaty of 1911 was a catastrophy for the Masai and that they were tricked by government into giving up good land for bad. It is also pointed out, however, that as a result of the treaty of 1911 the Masai received over twice as much as they lost, and that land included some of the finest grazing and forest land in Kenya. The treaty was requested and signed by the Masai leaders. As a result of that treaty, their population density in the reserve was probably about one and one third persons per square mile, so in terms of land, this treaty made the Masai one of the richest tribes in Africa.

175 Regardless of the logic, the move was resented

175 strongly by many of the Masai involved. Few of those
who made the move are still living, but the memory of
175 it is kept alive by the Masai nationalists. The Masai in
181 Kenya's Western Masailand are, or are descended from,
184 those who made the move from Laikipia. They are characteristically more conservative and more distrustful of the government than other groups of Masai, and they attribute these attitudes to the move.

Fosbrooke (1948:11), an admirer of the Masai, attributes the conservatism of the Tanganyika Masai to their hardships from famine, pestilance, civil war, and German administration in this way:

> It is almost impossible to find at the present day an elder who did not go through considerable hardship in his youth. To anyone who has lost and regained a possession, such possession is of greater value, at least sentimentally. The Masai of Tanganyika lost their cattle, their mode of living and their tribal life, and largely by their own efforts have once again regained them. It is suggested that their intense conservatism and resentment of change may perhaps be better understood in the light of the foregoing.

175 During the German period the Masai were
648 largely excluded from the Western Masailand in Tanganyika,
131 although occasional raiding parties came through it. Between 1900 and 1905, according to Grant (1957), there was one Masai encampment or warrior's barracks

175 648 131 at the Moru Kopjes on the western edge of the Serengeti Plain, just north of the headwaters of the Simiyu River (Fig. 3).[1] Western Masailand in Tanganyika is large and was virtually uninhabited by Europeans, so doubtless some Masai remained throughout the German period.

During the 1914-18 war the Germans retreated from northern Tanganyika. The Masai whom they had evicted began returning to their former grazing grounds. In addition, by the end of the 1914-18 war Masai from Kenya had penetrated the Serengeti region and the Ngorongoro Highlands. Part of these were from the Purko section, people who as a result of the 1911 treaty had moved from areas around Lake Naivasha to the Loita Plateau north of Loliondo. Others were of the Loita section who formerly lived on the Loita Plateau.

When the English took over Tanganyika as a Trust Territory after the 1914-18 war, they established all of Tanganyika Masailand as a single Masai District. Its headquarters were at Monduli, about 15 miles west of Arusha (Fig. 1).[2] In the study area the western boundary of the Masai District is the line between the Lake Province and the Northern Province (which includes the Masai District). This line was drawn by the Germans

[1] [See p.19.--Analyst]

[2] [See p. 9a.--Analyst]

175 and it cuts through the Serengeti Plain roughly paralleling
648 the eastern border of the Serengeti National Park (Fig.3).
131 Grant (957) notes that the line is an arbitrary one which did not take account of the actual distribution of the Masai. The Serenget section of the Masai formerly occupied the plains west of the line. When the Germans surveyed the area they apparently thought it uninhabited because the Masai had been dispersed by famine and civil war. After the 1914-18 war the Serenget Masai returned to the western Serengeti. They were then in Lake Province but they were so isolated from its administration that the District Officer for the Masai District at Loliondo handled their administration.

In 1920 the English administration evicted the immigrant Kenya Masai from Tanganyika in favor of the resident Kisoongo section of the Tanganyika Masai. Since then the Kenya Masai have been moving southward again slowly.

*13 Early in German times the importance of the
648 unique wildlife concentrations in the Serengeti and Ngorongoro Crater were recognised (Grzimek and Grzimek, 1960a). During the period between the wars the Tanganyika Government created several nature reserves in the area protecting some of the wildlife from hunting, but not much affecting the Masai.

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In 1940 the Ngorongoro Highlands, much of the Serengeti Plain, and a strip of bush country leading to Speke Gulf were gazetted as a National Park. Due to the war and the terms of the ordinance this action did not affect the area or the Masai living there. In 1948 because of renewed interest in the status of the area, a new National Parks Ordinance was passed, and later, by Government Notice No. 137 of 1951 the area was re-gazetted the Serengeti National Park.

At that time it was believed that the objectives of a national park as defined by the London Convention of 1933 (C.C.T.A., 1953), could be achieved and maintained with a resident population of Masai with their livestock. In a few years it became evident to both the Masai and the Government that the arrangement was not working out. The activities of the Masai and their administrators were conflicting with those of the national park staff. There followed a series of hearings, government announcements, and interventions by interested individuals and organizations, culminating in 1956 in the appointment by the Tanganyika Government of a Committee of Enquiry. The Report of the Serengeti Committee of Enquiry (1957) details the history and events leading up to the enquiry. Further comments on and analyses of the situation include those by Anon. (1959), Bigalke (1959), Boyle (1956),

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648 Grant (1957), Grzimek and Grzimek (1960a), Kenya Wild
656 Life Society (1957), Huxley (1961), Pearsall (1957),
659 Petrides (1956), Talbot (1956), the Tanganyika and Kenya
Wild Life Societies (1956), and Thomas (1960).

In 1959 and 1960 the park regulations and boundaries were revised (Fig. 3)[1] and the Ngorongoro Conservation Unit was created. The new regulations for the park exclude human residents and livestock. The Conservation Unit covers some 3,000 square miles adjoining the park to the east and south, and includes the Ngorongoro Highlands and part of the Serengeti Plain. The purpose of the unit is to achieve a balanced management of the resources and to develop the natural resources of water and grazing in the interests of both human and wild life populations.

Since 1959, then, the Masai have been excluded from the portion of the western Serengeti Plain and the bush country to the north that is within the park boundaries. The park boundary was adjusted several times to exclude from the park various water holes around its periphery that were considered important by the Masai. As a result the western park boundary follows a zig zag line from the southern Serengeti Plain north to the

[1] [See p. 19.--Analyst]

*13 Kenya border. The only significant area lost by the Masai
648 was the Moru Kopjes area. This was used occasionally
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659 during the dry seasons because of the springs and good
grazing found there. By about 1956, however, the last
spring appeared to have dried up because of destruction
of the vegetation by the Masai.

*13 The status of the Masai in Narok District has
184 remained relatively constant compared with that of the
Tanganyika Masai to the south. Since 1911 the only
changes have been slight enlargements of the area and
fluctuations in the land infested with tsetse fly.

*13 The part of Western Masailand immediately to the
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224 north of the Serengeti National Park and east of the
65 Siria Escarpment (Fig. 3) is Kenya's finest game area.
Following the Second World War part of this area, the
triangle formed by the Mara River, the Siria Escarpment,
and the Tanganyika border, was made a National Reserve.
This action protected the area from hunting but did not
affect the Masai. In 1961, due largely to the efforts
of Major Temple-Boreham, Senior Game Warden of the area,
and Mr. C. Denton, District Commissioner of Narok, an
agreement was made between the Narok District African
District Council and the Kenya Government to establish a
Masai Mara Game Reserve. The reserve covers some 700

*13 224 square miles adjoining the Serengeti National Park and
648 including the Mara Triangle. The African District
65 Council has appointed a warden and subsidiary staff
to the area, and has passed by-laws for its management
including control of burning and grazing. A section of
the reserve of roughly 200 square miles adjoining the
Serengeti National Park has been set aside as a Game
Reserve Developed Area in which no grazing nor entry
[529] is allowed except by permit of the warden. With
Government help they have built roads and a lodge, and
the proceeds from visitors' fees go to the Masai.
This is, in effect, a true national park run on a local
basis by the Masai.

Mode of Life

*114 Introduction and Methods: Customs and mode of life of the Masai have been described and discussed in some detail by Fischer (1885), Fosbrooke (1954, 1957), Gower (1948a), Grant (1954, 1957), Hollis (1905), Huntingford (1953), Leakey (1930), Merker (1904), Sanford (1919), Simon (1962), Thomson (1885), and Weiss (1910). There are also scattered observations on the Masai in the voluminous writings of hunters, collectors, and explorers such as Baumann (1894), Millais (1920), and Peters (1891). A further group of writers such as Gunther (1955) have published superficial and often erroneous accounts of the Masai.

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121 The purpose of this section is not to describe in exhaustive detail the customs and ways of life of the Masai, but rather to discuss briefly our observations on the mode of life of the Masai in the study area, as it affects the ecosystem.

12.1 Sources of Information: It is extremely difficult to obtain accurate, unbiased information about the Masai. As discussed above, most white persons who are acquainted with the Masai are strongly biased for or against them. Because of traditional or present raiding most Africans of other tribes feel strongly about them. Additionally, "city" Africans and those with overseas

121 educations usually regard them as savages and an embarrassment to the advancement of their country. Intentionally or otherwise, information from such sources is very likely to be biased.

123 [609] It is often difficult to get accurate information about the Masai from the Masai themselves. Being ulta-conservative and suspicious, the Masai appear to regard with mistrust anyone who is pointedly interested in them or their livestock, and anyone in government. Their answers are affected by this attitude.

124 123 Interpreters are another, often-unrecognized source of misinformation even for the objective investigator. Whether the interpreter is a Masai or is from another tribe his interpretation may be affected by the factors discussed above. Interpreters frequently "interpret" what they think will please the questioner out of politeness and a desire to please. Occasionally interpreters misinterpret for other reasons. When the language interpreted was Swahili which I understood I have heard interpreters misinterpret when the true answer would have involved the interpreter in more work or an arduous journey. Another good example is the African who interpreted for an American anthropologist who spent several months living with the Masai, but did not learn

123 the language well. After the anthropologist left, the 124 interpreter joyously told people how he had misled the American who had carefully written down the tall tales he had "interpreted" for him. Subsequently this "information" appeared as a learned dissertation.

124 Difficulty in understanding the langauage is another problem, whether or not an interpreter is involved. An extreme example of this problem comes from the story of a high government official who was giving a speech about soil erosion to the Masai. He spoke gramatically perfect Coastal Swahili, which differs from the Up Country Swahili spoken around Masailand. Ending his speech on the theme that steps must be taken quickly to remedy the problem, he pointed dramatically to his watch and said, "The sands of time are running out!" The interpreter said," The Bwana says his watch is broken in the sand and he must go quickly."

Bearing in mind the above problems, although we have learned from discussions with Africans, Europeans and the Masai themselves, our information is based primarily on our own observations.

*122. Our relationship with the Masai: We speak very 124 little of the Masai language but we do know Up Country Swahili.

124 [191] Swahili. Many Masai in the area speak some Swahili, so using Swahili and a limited number of Masai nouns we usually could converse with Masai throughout the study area. Occasionally we had the services of interpreters.

123 [609] These Masai regard visitors in their country with interest and guarded suspicion. The suspicion is greatest if they believe the visitors are representatives of the Government. After we had lived on safari in Western Masailand for some months constantly moving from place to place the Masai appeared to accept us as a harmless, neutral, and occasionally interesting phenomenon.

Our status with them was helped by our work
[231] with grass and animals. Above all else the Masai appear
[181] concerned with animal husbandry. They have a lively interest in wild animals, appreciation for domestic livestock that is almost reverence, and an understanding of the importance of grass. Our work on these things therefore seemed understandable. Beyond the frequent initial query: were we with the Government, there was never any question of why we were working there. The Masai appear to accept without question that white men are prone to the strangest behavior. Movie companies and some tourists fortify this conviction.

123 Our use of the capture gun to capture and mark
824 wild animals was of particular interest to the Masai.
123 They would often come up to watch us. Masai are famed
461 for their refusal to carry out manual labor of any sort
824 hence are regarded in East Africa as poor helpers on
safari. However, labor, where it involves animals,
is another matter. Sometimes Masai would come up and
voluntarily help us handle captured animals, and this they
did very well. We even experienced Masai coming to our
camps to talk about our capture work that they had
observed from a distance.

123 When we had extra meat from animals that we
262 collected, we took it to the nearest Masai village.
609 Most writers have reported that Masai will not eat the
meat of most wild animals. We found, however, that
they gladly accepted it in most cases. They always
wanted to know what animals were involved. In several
cases, when we first approached a village those who came
out to meet us would refuse the meat. Then someone
who knew us or knew of us would appear and accept the
meat, explaining that the others did not know us.

123 Virtually all visitors to Masailand are regarded
757 as a sort of travelling dispensary by the Masai. This is
true throughout the world for most people who do not have

123 757 *[114] medical supplies. We had frequent visitors wanting "dawa," medicine, or a "sindano," an injection. The latter we could not provide (although we had a camp helper who stole a hypodermic syringe and for a time had a good business selling injections of water or anything else handy). We did serve as emergency hospital for various injuries, large and small. One warrior came to camp with his hand nearly cut in two. He refused to go to the hospital at Narok, so my wife somewhat reluctantly and dubiously repaired the damage. Several months later when we returned to that campsite, the same Masai came striding across the plain and proudly showed his healed hand. He was profuse in his thanks and wanted to bring us some goats and sheep as a token of his gratitude.

123 829 The Masai greatly enjoy riding in a vehicle. They are willing to walk several miles just to have a ride. Whenever it did not conflict with our scientific work we made it a point to give them rides. These were often odoriferous but always interesting experiences. We learned much about the Masai from them and we became well known to the many villages involved.

123 721 The Masai's apparent acceptence of us as essentially a part of the landscape is illustrated well by an incident in the southern Serengeti Plain. We had camped

123 beside a trail near a Masai village. In the early morning
721 a party of Africans from nearby Sukamaland raided the Masai village, killing at least one man and making off with the cattle. At dawn the Masai discovered their loss and ran off in full war regalia to intercept the raiders. Their route took them right through our camp where we were eating breakfast. Coming at a full run with spears and shields they looked rather fearsome, but as they passed they all waved and shouted greetings. shortly thereafter they caught the raiders and bloodily recovered their stock.

123 Being in the position of neutral, nomadic
124 residents it seemed perfectly appropriate and natural for us to casually discuss mutual interests including livestock, grasses, weather and wildlife with passing Masai, and vice versa. Consequently our status in the area helped us greatly in obtaining information. What we were told by the Masai agreed with our own observations, and was often at variance with what they told visiting anthropologists and others.

*233 Social Organization: The Masai in the study
[221] area are essentially semi-nomadic pastoral people. Their
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*233 [231] Their livestock, described below, consist of herds of cattle, sheep, goats and donkeys. The Masai way of life revolves around the grazing and water requirements of their livestock.

621 561 614 177 178 Their principal units of social organization, as they affect this discussion, are sections, age grades, villages, and families. Clans have an important place in ethnological discussions and in some areas they determine matters such as water rights (Fosbrooke, 1948). Our impression is that throughout most of Western Masailand the concept of clans is of more ethnological than ecological interest. One basic reason for this is the effect of the Government administration in Western Masailand.

. . . . With the physical and social upheavels in both Kenya and Tanganyika from the 1880's through about 1920, the establishment of African District Cou[illegible]s (District-wide governing bodies), creation of the park and conservation unit, and various development projects, the clan and other social units have been greatly disrupted. Grant (1954, 1957) describes this effect in some detail for the Masai in the former boundaries of the Serengeti National Park.

[i.e., the Masai.--Analyst]

614 634 (a) Section: A section is defined by Fosbrooke (1948:7) as: "a territorial unit of the Masai, the members of which regard themselves as owners of the waters and grazing grounds, to the exclusion of other sections. Such a unit is called ol osho, pl. il oshon. Alone or in groups the sections function as units in war, in allegiance to a particular Laibon, and in the performance of certain tribal ceremonies; in general they possess a sense of solidarity which expresses itself in regarding members of other sections to a certain extent as strangers."

131 614 634 Most of the Masai in Western Masailand in Kenya are of the Purko section. The Loita section live on the Loita Plateau. Three small sections, the Moitanic, Uasin Gishu, and Siria, live above the Siria [433] Escarpment. The first two are at least partly cultivators. In Tanganyika, the Serenget section occupies the Serengeti Plain (which was named for them), and the Salai section lives in the area between the Serengeti Plain and the Rift, including the Ngorongoro Highlands and the 614 634 southern Loita Plateau. There are a number of subsections and divisions of these main sections. The original section organization has been much altered. Grant (1954) describes in detail these alterations for Tanganyika.

... for Tanganyika.

561 181 (b) Age grade: The age grade system is of great importance in the life of a Masai man, since it regulates his conduct toward other men and women and is the baisis for the political organization of the tribe. The system is also of significant use in dating past events (Fosbrooke, 1954).

721 181 Warfare was of great importance to the Masai prior to the 1900's. The whole social organization of the tribe was built around the production and maintenance of an effective fighting force. Although actual fighting is relatively rare now, the customs and social organization remain basically the same.

857 *233 881 561 701 Until his early teens the primary duties of a boy are herding livestock (Fig. 9).[1] Roughly every seven years there are a series of ceremonies culminating in a circumcision ceremony. This ceremony is taken by all the young men of the correct age (roughly in their mid teens), and it produces a class of warriors each of whom is known as ol-murrani, or moran. This is considered the most important occasion in the life of a Masai man, and from then on he is a full member of the tribe. Each group to be circumsized is given an age

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[1] [See p. 53.--Analyst]

561 class name, and is allied with the next (or previous)
701 [881] group, the first being the right hand grade and the other
being the left hand grade. After several years the
[884] junior warriors go through another ceremony and become
full warriors. Their total period of warrior duty may
714 be about 15 years. The warriors are distinguished by
their hair style and spear.

714 The hair style involves a complicated
302 plating of the hair with some combination of cords,
pieces of hide or gut, bark, or stick; all liberally
plastered with sheep or cow fat and red ochre. Elliott
(1948) has detailed the methods and materials used and
variations in style between areas.

714 The warriors' spear is often over five feet
411 long. It has a long, narrow, double-edged blade, an
equally long but round and pointed tail, and between
them a very short wooden hand grip serving as a shaft.
Warriors also carry a flat, double-bladed long knife or
short sword called a simi. These useful weapons are
177 carried at the waist in a red leather sheath. Originally
411 the metal weapons were produced by metal-working tribes.
326 They now come from England and the first thing a moran
does after buying a spear or simi is to file off the
411 brand name. When in ceremonial dress or at war the

441 warriors also carry a narrow oval shield made of buffalo
or giraffe hide on a wooden frame, and painted with
insignia including the warrior's age grade and clan.

561 Originally during the period of warriorhood
701 the morani were not expected to do any work except
[712] fight. They lived in a separate village, called a
[562] manyatta, and were generally taken care of by the
[836] unmarried girls of the tribe. Discipline was reputed to
have been extremely good. The warriors had older
advisors whom they obeyed.

224 Ostrich's were hunted to obtain feathers
[225] for ornaments, buffalo and giraffe for shields, and lion
[301] for the highly prized mane. Traditionally the moran
[411] was expected to blood his spear on a lion. The dramatic
177 Masai lion hunts are famous. (Simon, 1962). At
178 present warfare and lion hunting are illegal. The obvious
561 result is a large body of young men with absolutely
701 nothing to do for a period of up to 15 years of what
224 could be the most energetic period of their lives.
721
*[233] They tend the livestock some, but much of the time there
is nothing for them to do. As a consequence discipline
is breaking down. The elders apparently have much less
influence or control over the morani than they did

177 178 224 561 701 721 previously. There is a considerable amount of raiding to steal stock from surrounding tribes. This precipitated several minor wars when we were there, and administrative action prevented one major war with thousands of combatants. Some lions are still killed, and the morani have been blooding their spears on a variety of other animals, most notably rhinos.

561 Following the period of service as warriors, each age class goes through another ceremony. Two age classes, a right hand and left hand together, take the ceremony and they then receive another age grade name which they retain the rest of their lives. Thus these elder age grades each span a period of about 15 years (Grant, 1957).

177 178 561 Periodically the administration has tried to discourage the moran system. In late years some of the elders have also tried to change the system in order to maintain better control over the young men. The system still continues in Western Masailand but it is much less regular than previously.

561 593 591 When a warrior becomes circumcised he may take his mother with him to the warrior' manyatta, or he may leave her home or apparently even stay home himself.

561 He may marry when he is a senior warrior. When he becomes
593 591 an elder he may take his mother (if he wants) and her
[582] share of the family cattle (for each wife has a given
[422] share of cattle) and move off to join others in a village
[562] (Fosbrooke, 1948).

561 The unmarried girls of the tribe live in the
836 warrior's manyattas and normally each moran has one
[583] favorite girl who becomes his concubine. They told us
that usually that girl became the warrior's first wife.

621 *(c) Villages:* Villages consist of a group
of families, often about five but sometimes more or
less. The villages are commonly called *bomas* or
361 (improperly) *manyattas*. Each boma consists of an outer
*233 circular thorn fence with a series of gates, one for
[417] each Masai elder. Within the gates there are a series of
huts. Often around the huts are small thorn fences
in which young livestock are kept. The cattle of the
village are normally herded into the space in the center
of the boma each night for protection from two and
four legged predators, and in the morning they are taken
back out to graze.

595 When a Masai marries, his first wife builds
on the right of his gate, his second on the left,

595 and so on. The wife is given a specified number of cattle to keep in trust for her son, and she and the children also tend young animals in the herds.

342 These huts are about five feet high and of varying dimensions, but usually roughly square and 10 to 20 feet across. The door is very low. Just inside the door there is normally a baffle wall of loosely woven twigs. Beyond that there are often two or three rooms, each divided from the others by a low open wall of
[231] twigs. Young livestock are brought into one of the
[513] rooms and the others serve for sleeping and cooking.
[352] Usually the beds are platforms of twigs and grass covered
[354] by hides. The cooking fire is in a far corner and is very small, normally with three stones around it to support pots. There is no smoke hole in the roof. The outer walls and roof are an open mesh of wattle often interwoven with coarse grass and shrubs. Support comes from larger branches and small logs up to about six inches in diameter. The exterior and walls and roof, and the insides of the door opening are plastered with
[184] a mixture of mud, cattle dung, and short grasses. Hut
[462] design varies slightly from area to area. Constructing the huts is women's work. Men occasionally help in collecting larger trees and bushes.

13*
361
[342]
Building a large boma entails cutting a large number of trees (Fig. 22). Where trees are thick in Western Masailand there are tsetse flies (Fig. 23). Consequently the bomas are constructed away from them in more open country, in open grassland near to hills or watercourses or in open parkland. Under such conditions a large boma can result in the clearance of larger woody growth -- for initial construction, subsequent repair, and for fires -- from an area ranging from about several dozen acres to a square mile.

361
*233
221
Fosbrooke (1948), Grant (1957), and Page-Jones (1948) have noted that the Masai normally placed their dry season bomas within about five miles of permanent water. One day they graze the animals to and from water, letting them drink. The second day they graze the opposite direction, and on the third day they return to water. Thus a rough circle with diameter of ten miles is grazed around each boma. In the wet season the Masai leave the boma, either setting up a new one in an area of good [887] grazing, or making temporary camps (Ibid.). Occasionally old people with a few milk cows are left behind in the main dry season boma. Under the present conditions in Western Masailand we saw very few large bomas that were 342 not located at permanent water. It may be that increases 343 in stock, or decreases in available water, or some other
*233

[TEXT CONTINUED ON PAGE 133]

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362

Figure 22.

Abandoned boma site in Acacia woodland north of the Serengeti Plain. This was a small boma, abandoned for two years. The remains of the boma are behind the Land-Rover. Note the numerous stumps of Acacias cut for construction of the boma and for firewood; the sprouting from the stump in the foreground; and the ground cover of weeds and coarse grass. The palatable bunch grasses were killed out by overgrazing before the Masai left.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

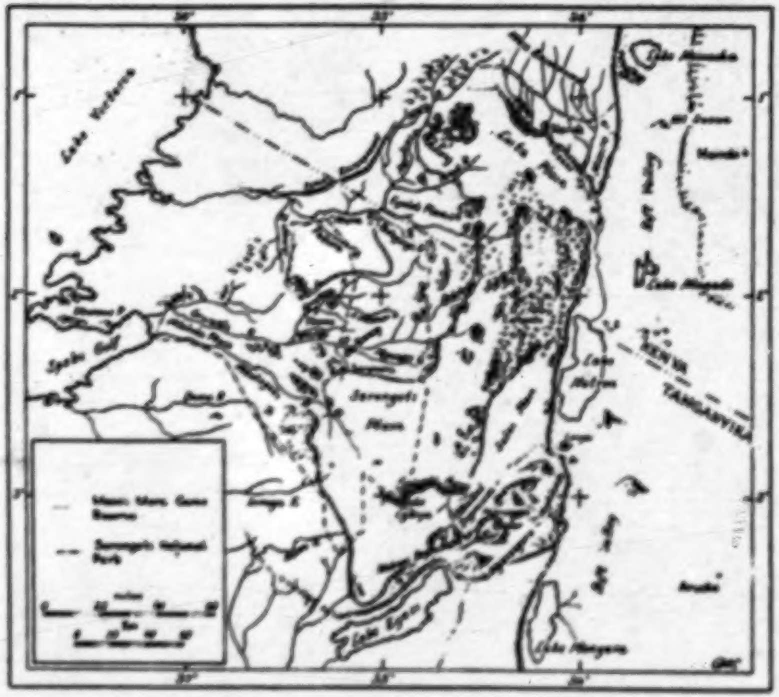
#13
102

Masai:

Dry Season ... ●

Wet Season ...

Tsetse Flies: /



Lake Victoria
Speke Gulf
Serengeti Plain
Lake Natron
KENYA
TANGANYIKA
Lake Manyara
Lake Eyasi

Figure 23. Distribution of Masai and Tsetse Fly, 1961.

342 factor has changed the Masai pattern of boma construction.
343 *233 The present bomas, for the most part, are semi-permanent
and during the rainy season the herds are sent out to
graze in the care of a few youths supervised by one or
more elders. They construct temporary brush bomas,
just large enough in diameter to contain the stock in their
care. Usually no plastered hut is constructed. Instead
a small, often open-roofed brush enclosure is made in
one corner. Where a temporary boma is to be occupied
for several weeks a somewhat larger boma is made and the
hut may be plastered. Building these temporary bomas
results in some brush clearance, but rarely in any tree
damage.

362 Large bomas appeared to be relatively
[361] permanent. When a large boma was abandoned another was
usually built nearby, often only a few yards away.
Individual bomas appeared to be occupied normally for
about five to eight years, although some doubtless
last longer. One cause for moving is the accumulation
*[233] of dung. In the center of large bomas where the livestock
are driven during the night the dung accumulates into
a gentle hill sometimes several feet high at the center.
[364] This creates sanitary problems in the rainy periods since
the huts are at the foot of this hill and the doors
usually face inward. When it is dry if a fire gets

362 started in and under the dung it is similar to a peat
fire and virtually impossible to put out.

708 · Masai also sometimes abandon a boma, or
at least the house involved, if a person dies in it.
751 People who are very seriously ill are removed from the
boma at least during the day, often to a small thorn
boma with a shelter constructed nearby. They may remain
there at night also. It was difficult to learn much
definite about this practice. A disabled person spending
the night outside a boma is very likely to end up
[177] inside a hyaena. The administration frowns on this
[178] efficient method of disposal and consequently the Masai
have become reticent to talk about it. The sick persons'
bomas that we saw looked to have been occupied nights
as well as days.

262 **Food:** Traditionally the Masai are supposed to
survive entirely on blood and milk (Gunther, 1955). In
Western Masailand the Masai diet consists of posho
234 (maize meal), milk, meat, and occasionally blood. The
462 cows and sometimes goats are milked by the women and little
234 girls. The milk is collected in large calabashes. These
415 calabashes, ochre colored and sometimes ornately
[531]
[386] decorated with beads, are almost as much a symbol of the
[291] Masai as the ochre blankets or cloaks, moran spears and
hair styles.

234 hair styles. The gourds are grown by nearby cultivators
415 [264] and purchased or traded by the Masai. The calabashes
are cleaned between usings by washing in water (if
available) and then purified with a mixture of urine and
wood ash. After being carried in one of these containers
the milk has a rather characteristic, somewhat smoky-sweet
taste that may stay with one for several days.

443 The maize meal is purchased or traded from the
dukas or trading post cum general stores which are
found at Narok, Loliondo, and at other points around
the periphery of the area.

262 272 Meat comes from the Masai livestock and occasionally
game. The old traditions laid down specified rules for
who in the tribe might eat what kind of meat, and at
[701] what times. Apparently the warriors had a right to
demand milk and sometimes meat from anyone, at least
in their section. Milk and meat were not to be consumed
on the same day, but blood could be mixed with the milk.

701 When not fighting the warriors could carry out
[562] an olpul, or meat camp. They would take goats or a
bullock and make camp in the bush, kill and eat the
animals. The olpul might take from a week to a month,
[826] depending on the available time and meat. We presume that

701 the principle was that the meat and blood strengthened
[826] the warriors for fighting. We periodically came upon
[252] moran cooking fresh meat. It was usually goat or sheep,
although occasionally bovine, and they cooked it either
by skewering pieces on green limbs which they held over
the fire, or by placing the strips of meat on a wooden
[857] grill above the fire. Youngish children usually
701 accompanied the moran. Gower (1948b:79) notes that in
562 Tanganyika Masailand:

> At an olpul a few moran (warriors) will go into the bush and slaughter a bullock or goats. They take with them a few uncircumcised boys and girls. They camp in the bush for any period from 10 to 30 days, depending on how many bullocks they have to slaughter. For the first few days they eat the meat roasted and cooked; thereafter they subsist on soup. The Masai consider that this diet gives considerable strength.

We never observed moran cooking meat far out in the bush. Usually these feasts were close to a boma.

We were told that eland and buffalo were considered
close enough to cows to be proper food for Masai and
this was also postulated by Grzimek and Grzimek (1960a)
562 and described by Huntingford (1953:109). The women
[843] apparently could eat game meat, especially gazelles,
during pregnancy. From the reception of the meat we
brought to bomas, we believe that in addition to women
and children elders and a few moran will gladly

562 eat meat from wildebeests and gazelles. When I shot an
elephant near one boma the Masai women turned out in
[252] force. They spent most of the day cutting off strips of
[462] subcutaneous fat and some flesh. A few elders joined
[825] the women in the cutting. Several Masai requested fat
from a lion I had shot (which had been raiding their
boma), but they said that their use was for medicine
rather than food. We have records, therefore, of
Masai eating (or taking to eat) wildebeest, Grant's
gazelle, Thomson's gazelle, elephant, buffalo, eland,
and kongoni.

Cattle are usually eaten when they die. Cows
are rarely slaughtered, although bullocks sometimes are
killed for food and prize ones are killed and eaten
[562] by men at ceremonies. We have watched women picking up
the remains after livestock have been slaughtered, and
Millais (1920) spoke of Masai women eating offal and
other remains of oxen or sheep after the men were through
eating.

231 Bleeding of cows and sheep is accomplished by
272 tying a thong about the animal's neck so the jugular
swells, then shooting a partially blocked arrow into the
jugular vein and catching the spurting blood in a gourd.

231 272 When they have enough blood, the thong is released and the small wound covered with mud or dung, and the animal runs off apparently none the worse for wear. The blood is drunk warm, or mixed with milk.

146 Although they are thin, the Masai appear adequately nourished, and they have great physical endurance. The Ministry of Health doctors told us that Masailand was the only part of East Africa in their experience where the children did not show signs of Kwashiorkor or the other diseases of malnutition that are so common with Africans. Gale (1960) noted that the greatest defect in the diet of the East Africans is lack of animal protein, but this is true of the Masai only in times of extreme drought.

291 [386] Clothing, Jewelry and Utensils: The traditional clothing of Masai men and women is an ochre colored cloak of cloth, usually gathered over one shoulder. Some wear (292) skins, usually of sheep. A cow hide is used for a rain coat. Most Masai men wear sandals made from heavy leather or old rubber automobile tires. Very little else is worn by either Masai men or women, except near missions where the women occasional /wear more concealing cloaks.

301 Women and occasionally men wear necklaces of
beads. Women have ornate jewelry consisting of rings,
beads, beaded bracelets, and wire loops around their
[304] neck, wrists and ankles. Both men and women pierce and
stretch their ear lobes; the women wear large ear
bangles through them and the men use them to carry
snuff containers or other articles about the size of
a 35 mm film casette.

411 Spears, simis, and knobkerries and shields may
[714] be carried by the men. Elders often carry a long staff
[561] instead of a spear. Cooking utensils are simple, some-
415
[513] times consisting of a few pots and pans. Bedding consists
of hides, with sometimes a blanket. The gourds mentioned
492 above are always present. When moving from one place
to another a pack saddle is used which consists of two
large (two by three feet) flat rounded plates made of
sticks bound and laced by leather thongs. These are
tied above and on either side of the donkeys' backs,
giving the appearance of semi-folded wings. Hides,
lodgepoles, cooking utensils, and other kit are placed on
443 the donkey's back between these. Trade goods are
purchased or traded from small dukas around the edge of
the area or more recently from itinerate traders who
visit the larger and more accessable bomas in trucks.

Animal Husbandry

+233 It is widely believed that since the Masai are a pastoral people whose life revolves around their livestock, they are, therefore, experts in the arts of animal husbandry. If the success of animal husbandry is judged by the numbers of animals kept during years of good rainfall and forage, and the importance attached to those animals then the Masai are successful in animal husbandry. If, however, success is judged on the quality of the animals, their survival in drought years, and management of the range so that productivity is not lowered through overgrazing, then from the evidence we have seen the animal husbandry of the Masai is very poor.

Prior to European times the grazing pattern of the Masai livestock must have been very similar to that of the migratory wild ungulates. In the wet seasons when there was plenty of water they could graze over a wide area. In the dry seasons they retreated to permanent water. The numbers of livestock a Masai could keep were limited by disease, predation, raiding by other Masai or Africans of different tribes, water, and food supply.
221 +233 The Masai were nomadic, in that they moved about following forage and water for their animals. From the evidence of Fosbrooke, Grant, and others, this movment of the

221 *233 Masai was not an unoriented wandering but it was instead a regular seasonal movement *from* one established area *to* another, and back. In this sense the movements of the Masai fit the definition of animal migration -- "seasonal and regular passages..." given by Bourlière (1955:203). Each social group apparently had a dry season water supply near which they maintained bomas, as described above. In the wet seasons some of the tribe took the livestock away to take advantage of the more abundant [614] grass, and water in other areas. Since there were well defined areas belonging to or controlled by different clans or sections (Hollis, 1905), the wet season movements of the individual Masai must have been relatively circumscribed. This is the case at present in Western Masailand. Each village has an area where it sends its livestock during the wet season in addition [628] to the water near the base boma. Although these wet season areas may be changed periodically, there is some sort of agreement between different villages regarding division of available grazing, and disputes arise when one village's area is invaded by another.

*233 It appears to us that both in former times and at present the absolute limits to the numbers of livestock a Masai could keep and the pattern of his grazing

*233 management were determined primarily by water and disease. Of these two factors, water appears far the more important.

Water: It is clear that water is basic to the survival of the Masai and their livestock. There is an upper limit to the number of animals that any one water source can supply, and it is the dry season water source that is the primary limiting factor here. The Masai believe it essential to water their livestock at least every other day, except in times of extreme emergency (Page-Jones, 1948; Grant, 1957). This belief is widely held throughout the European ranching community in East Africa also. The location of bomas, much of the Masai mode of life, and their animal husbandry is organized on and around this assumption.

*233
232 Experiments carried out by the East African Agricultural and Forestry Research Organization under the direction of Dr. W. Payne are showing that in Masailand, cattle which are provided water only once each three days and which walk up to about 15 miles to get that water can survive drought conditions as well or better than those which are given water each one or two days near their forage.(1)

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(1) A preliminary report on this work was presented by Payne, Southon, Bazin, Hutchison, MacFarlane, and Horrocks at the 8th International Congress on Animal Production in

*233 232 Hamburg, Germany, but I do not have the reference available. The experiment was outlined by Payne (1961) and part of the results presented by Livingston, Payne and Friend (1962).

If the Masai were indeed good animal husbandmen, it is surprising that they have not discovered this fact in the 400 or more years they have been herding
181 cattle in East Africa. The fact that they apparently
*233 have not is probably due to their intense conservatism,
232 particularly as it affects their cattle. Evidence such as this points to the deep seated conservatism that antecedes their periods of stress in the end of the last century, to which Fosbrooke (1948) and others have credited present Masai conservatism.

*233 Water supercedes all other considerations in Masai grazing management. In periods of extreme drought the Masai will take their cattle into areas infested with tsetse fly if water is there, preferring to accept some mortality from disease than greater mortality from thirst. The same consideration governs their moving stock into areas where the grazing rights belong to other groups or tribes, or into areas where the danger of wild predators is greatest.

232 Disease: Disease periodically decimated Masai livestock even before the introduction of rinderpest.

232 Thomson (1885) describes visiting an area where some cattle disease had killed many of the cattle. The Masai recognize several cattle diseases and reportedly (Grant, 1957) had their own methods of dealing with them before the introduction of modern veterinaries. In the case of rinderpest, when one village has a mild outbreak, Masai from other villages allowed their cattle to catch the disease to innoculate them. Most other veterinary medicine appears to have been preventive.

Snotsiekte, or bovine malignant catarrhal fever is a disease known world wide which causes high mortality in domestic cattle. The Masai believe that their cattle will contact this disease if they graze where wildebeests have calved. They say that the disease comes from the afterbirth of the wildebeests, or the short baby hair that is shed when a wildebeest calf is several weeks old. Work was undertaken at the East African Veterinary Research Organization to define the causal agent of the disease, its characteriestics, and the relationship between the wildebeests and the disease (Plowright, et. al., 1960). This work has shown that the wildebeests do serve as a reservoir of the disease, which is caused by a virus, but that the disease does not appear to affect the wildebeests themselves (Ibid.).

232 The method of the Masai to prevent the disease is to move their stock away from the areas where wildebeests are calving. They also occasionally attempt to drive the wildebeests away from the cattle, or keep them out of areas occupied by cattle. Grant (1957) has noted the latter, and at the time of wildebeests' calving we observed Masai driving herds of wildebeests away from their cattle.

"Nagana disease" or trypanosomiasis is carried by tsetse flies. The flies carrying this disease have been such an important factor in the ecology of the area that they are discussed at greater length below in a separate chapter. Areas occupied by the fly are avoided by Masai when grazing their cattle, although sheep and goats are not affected by the disease and they are grazed in such areas. The Masai method of coping with the disease is simply to avoid it. They also alter the flies' distribution through burning (see below) but it is questionable to what degree this effect is intentional. The veterinary departments are now providing the Masai with anti-trypanosomiasis drugs which to some degree allow them to graze in areas previously denied them.

232 East Coast fever is a tick-born disease of cattle. It is widespread throughout East Africa. In European ranching areas the cattle are dipped weekly to remove ticks. This is not possible with most of the cattle in Western Masailand, hence the Masai avoid the areas where the danger of the disease is heaviest. The disease appears to flare up at irregular periods, and certain areas are known to be particularly dangerous. One such is the lower slope of the Ngorongoro Highlands near Endulen. The Masai believe that the disease is caused by infected grass (Grant, 1957) and they fight the disease by burning the grass and grazing sheep and goats intensively.

Various other diseases periodically affect Masai livestock. In most cases the reaction of the Masai to diseases of livestock is first to avoid the area involved, if at all possible, and secondly to burn.

*233 Herding and Control of Livestock: Masai livestock are herded and grazed in characteristic tightly packed groups (Fig. 24 and 25). The compactness of these herds makes for easy distinction between domestic livestock and wildlife when seen at a distance. Presumably a tightly packed herd is easier for the herder to control and possibly a little less vulnerable to predators.

#13
#231

Figure 24.

Masai cattle. These are basically short-horn zebu cattle but with many additions of other breeds to the basic stock because of trading or cattle raiding. They are herded and grazed in tightly packed bunches which are quite destructive of the vegetation cover and soil surface, and aggrevates overuse of the most palatable forage plants.

#13
P233

Figure 25.

Masai sheep and goats. The long-legged meat goats tend to be lighter in color, while the Masai sheep are usually darker. The flocks are usually mixed. They are typically herded and grazed in tight groups much as the Masai cattle, with consequent aggravated damage to the grass cover.

#233 The cattle are very thoroughly conditioned to this herding pattern. Periodically some Masai cattle are purchased by veterinary departments, removed from Masailand, and put into experimental paddocks. Veterinary officers have told us that it often takes three or more years before these animals will move or graze in an open group instead of a tightly packed herd.

#13
#233 The principal ecological effects of close herding are to cause maximum destruction of the turf and soil surface structures from the animals hooves, and to subject the preferred species of grasses to extremely heavy use. This latter effect is intensified by the very slow speed at which the herds are moved while grazing.

#233 The Masai have remarkable control over their livestock. At many dry season water holes or wells they have constructed short troughs. Only a few cattle at a time can drink from these. On the commands of the herders the thirsty herds of cattle will stand back and a small number of animals will come forward and drink. When they are finished, they move off and another group comes forward. We have watched these water holes when up to six separate herds of cattle arrived simultaneously. They numbered something over 3,000 a232 herd. Each herd was stopped several hundred yards from the water hole. The herds were watered in the order of arrival, the first herd moving up to the hole, small groups drinking as above, then leaving and its place taken by the next herd.

a233 Numbers of Animals: The emphasis of the Masai
554 is on numbers of animals, not on quality, and certainly not on any balance between numbers of animals and range productivity. The animals represent wealth in the broad sense. Goats, sheep and occasionally cattle are traded for goods or sold. A certain number of cows are required for milk production. Beyond that, however, the Masai appear to regard cattle as a combination of status symbol, bank account, and object of reverence. The more cattle they have the better, and they see no point in selling cattle or trying to upgrade the cattle for that purpose. They do appreciate good livestock.
[554] Young boys often have a steer which they raise from a calf. They attach great importance to the condition of this animal. Still, wealth and status appear to be measured in terms of numbers of cattle, whatever their condition. Any effort to reduce these numbers seems to them a scheme to undermine their way of life.

178
a233 In former times the limiting factors mentioned

178 4 213 above made it difficult to amass large herds for any long period of time. The cattle numbers probably fluctuated greatly, depending on factors such as disease and drought. The English administration has provided excellent veterinary services, all but eliminating most diseases. They have provided water holes in otherwise dry areas to spread the grazing pressure. Predators have been killed wherever they [72] molest Masai livestock. Cattle raiding has been considerably reduced, and in Western Masailand most of the raiding is by Masai augmenting their herds from neighboring tribes, rather than vice versa.

With the other natural limiting factors largely removed and no artificial ones imposed in their place there has been nothing to stop the increase in herds but the carrying capacity of their rangelands.

4 273 291 In Narok District, for example, in April 1956 the cattle population was about 330,000 head (Dept. Vet. Services, 1956). By April 1958 the population had risen to about 378,000 head (Ibid.), and in May of 1960 it was reported at 450,000 head (Mann, 1960). This represented an increase of over 36 per cent in four years.

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231 In 1904 the cattle numbers in Masailand of Kenya were estimated at about 50,000, and there were an estimated 600,000 sheep (Simon, 1962). By 1961 the Kenya Masai had a population of 973,000 head of cattle, 660,000 sheep and goats, and a large number of donkeys, "at least double the quantity that their land will carry during normal conditions" (Glover and Gwynne, 1961).

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182 *Range Management of the Masai.* Grass is recognized by the Masai as being important to their livestock. But in general those in Western Masailand appeared to have surprisingly little appreciation of the types of grass that were preferred by their livestock or of the effect of varying grazing pressures on the grasses. There are Masai names for a number of the grasses. Yet many Masai in the study area only know a few of the more common ones. When discussing grass foods the Masai almost invariably say that the cattle eat *grass*, as do the wild animals. There appears to be little appreciation of the differing diets or well defined preferences exhibited by these animals (see below). When inquiring about the names or characteristics of various grasses the typical answer we recieved was to the effect that we were *fundis* (experts) on grasses, while they were *fundis* on livestock. They would then point out that in a herd of several hundred animals they knew

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232 each one. This example, in fact, provides an insight
182 into the emotional nature of animal husbandry of the
Masai.

13 The Masai realize that bush is encroaching in
232 many areas and that the forage is not as good as it
182
233 used to be, but this is explained as a shauri ya Mungu,
a matter of God's will, not man's. They will leave their
animals grazing on an area where there is water as long
as there is any grass left. The idea that overgrazing can
weaken or kill grass plants appears to be either foreign
to them, or it is outweighed by other considerations
unknown to us.

232 With the exception of burning, discussed below,
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233 we did not see a single example of any range management
activity that was not directly based on water or disease.

13 The original pattern of migratory or nomadic
231 grazing followed by the Masai duplicated that of the
182 wild animals. Under the environmental conditions of
Masailand it was and is probably the most efficient
and potentially most productive way to use the rangeland. As will be discussed below, under the semi-arid
conditions of Masailand many grasses cannot support heavy
year-long grazing while they can thrive under periodic

*13 heavy use. The ranching schemes put in for the Masai in
*233 Eastern Masailand illustrate this point. Water holes
182 were provided and areas were set aside for ranching projects. No real control was placed on the numbers of the cattle. The water allowed the cattle to remain in the areas throughout the year. Previously lack of water had enforced seasonal grazing with cattle and wild animals grazing the areas during the wet season and an almost complete rest during the dry season. Yearlong grazing quickly killed the perennial grass cover and without fuel for fires the brush encroached. Flying over Eastern Masailand now, one can easily pick out these grazing improvement schemes; they stand out as red blocks of bare, gullied earth.

Wherever yearlong water was provided for the Masai, they used it to increase their livestock numbers rather than to spread the grazing pressure of the existing livestock. The administration that provided the water did not enforce any limitations on numbers. Apparently all attempts to show the Masai the damage that overgrazing was doing to their own future ended in failure. Outside of a few particularly educated Masai, we know of none who appear to understand or appreciate the importance of the overgrazing problem.

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A several years' drought culminated in 1961, and as a result of the extreme overgrazing in Eastern Masailand, thousands of cattle and many Masai died. As was evident on the ground, and as clearly pointed out by many -- even veterinary officers (Waddington, 1961) -- the mortality was due to starvation on range depleted by overgrazing before the drought. There was plenty of water for the animals to drink. The mortality in the cattle of Eastern Masailand ran from 300,000 to over 400,000 head, and I was told that over 1,000 Masai starved to death also. In spite of this dramatic illustration, the Masai to whom I talked in 1962 blamed their difficulties on the will of God or the Europeans who appropriated their land.

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Masai Livestock: The Masai cattle of Western Masailand today are a mixture of breeds with short-horned zebu (*Bos indicus*) predominating. The Masai highly prize longer horned animals, and occasional herds will have a massive-horned Hamitic Ankole bull. It has been suggested (Payne,and Masai, verbal) that before the rinderpest epidemic of the 1890's the Masai cattle were predominantly long-horned. The rinderpest epidemic wiped out most of these animals, and the short-horn zebu, with its greater resistence to rinderpest, took their place. The short-horn zebu was introduced from

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*136 Southern Asia by both Arab and Indian traders following
231 the Arab invasion of A.D. 669 and it is still spreading (Williamson and Payne, 1959).

The present cattle represent what the Masai have bought, traded, or stolen since the 1890's. Since these processes, especially the latter, are still going on, the cattle appear very mixed. One can even see an occasional Holstein among the mixed zebu in Masai herds.

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231 I should be pointed out, however, that stealing
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721 is a relative term. According to the Masai, all cattle in the world belong to them, or at least were created for them. It appears that in their way of looking at things, it is not wrong to steal if the object is a cow; they are merely rectifying an obvious administrative error. Doubtless also the excitement and danger involved in a raid appeals to bored moran who have been brought up on stories of the glories of warfare.

*136 Occasional prize steers will weigh over 1,000 pounds,
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*233 but because of the animal husbandry practices the average weight of Masai range cattle is nearer 350 pounds. These animals require five to seven years to reach adult weight. The average liveweight gain per day is in the neighborhood of 0.3 pounds (Ledger, et. al., 1961). The cows will breed when about three and a half years old. These

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*136 same animals when removed from Masai care and put on good
231 forage may almost double their weight and growth rate.

Masai goats are of the long-legged meat goat type described by Williamson and Payne (1959). The average liveweight of adult Masai goats is probably between 40 and 45 pounds. The largest we saw weighed at the Narok slaughter house weighed 44 pounds. They attain their maximum weight at around 18 months.

Masai sheep are a fat-tailed, coarse-wooled animal whose color varies but dark browns predominate. Adult weights average around 44 pounds, but with better feeding they may attain 100 pounds. The largest we saw weighed was 85 pounds. On good forage they put on a liveweight gain of about 0.12 pounds a day for about 18 months. On satisfactory forage these sheep can have their first oestrus at about 9 months of age (Williamson and Payne, op.cit.)

Large numbers of donkeys are kept by the Masai
[492] in addition to their other livestock. The reason given for keeping them is for use as pack animals when bomas are moved. Occasionally they are used for carrying fire wood when the sources of wood are distant from the boma.

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231 We had the feeling, however, that donkeys just as other
554 livestock are a measure of success and security, and
regardless of the need some donkeys would be maintained.

*136 These donkeys are small animals whose weight
231 is probably less than half that of a wildebeest (i.e.
*233 under 200 pounds). They are quite independent. We
often saw the small herds of donkeys leave a boma
unherded and go to a water hole, then graze back to the
boma. This practice probably would not be followed
in areas where predators were common, but in the
peripheral areas it appeared to be the rule.

178 Large numbers of donkeys appear to have been
231 the rule for some time. Joelson in a general discussion
*233 of East Africa in 1928 referred (p.61) to the "Masai, who
graze immense herds of cattle, small stock, and
especially donkeys..."

*233
182 Burning
232 The Masai burn grass whenever it is dry enough
824 to ignite. The reasons they give for burning include
the following: It produces a flush of new grass
that is particularly palatable, nutritious and
easily available for their livestock. It clears the woody
growth and makes new grazingland. It clears or reduces
ticks, tsetse fly, and disease.

... ticks, tsetse fly, and disease.

*233 372 152 Burning grassland appears to be a deeply ingrained cultural trait. Young herdboys will seek out and ignite small patches of unburned grass, sometimes only one or two feet across. We have watched Masai moran striding across a dry plain lighting matches as they went, leaving a long line of small blazes gradually joining together behind them. We have watched junior and senior elders lighting fires, as well as boys and moran. We had marked plots that were burned as much as four times in one year. So we would add to the above explicit reasons for burning, the implied reason that they also burn simply because they get some satisfaction out of it.

182 372 [171] Fires are lit with matches. Possibly some are started from cooking fires that get away. Some fires, especially in wooded areas, are started by Wanderobo honey hunters (see below). But virtually all the fires whose origins we investigated were lit by Masai.

177 372 182 It seems probable that the coming of Europeans has altered the fire regime by providing large supplies of matches. It is far easier to light fires with matches than by using flint or other primitive means. With fires

122 easier to light more fires are lit, just as in the case
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372 of hunting tribes who have received firearms; with game
(182) easier to kill, more game is killed. Control in these
matters appears to be enforced by availability of tools
and difficulty of accomplishment, not by any conservation
ethic.

132 We questioned Masai, other Africans, and Europeans about lightning fires and never found the slightest evidence of lightning causing fires in the savanna country. There is no doubt that it ignites some fires in rim-rock or mountain areas, but we never even saw a lightning-struck tree in the study area. All the lightning we observed in storms was high, it occurred in heavy rain storms, or it was low in the region of Lake Victoria.

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232 There does not seem to be any discipline or
224 organization to the burning by the Masai. Fires are
*233 started in dry grass when herds leave an area, but they
are also lit when herds arrive in an area, if the grass
is dry enough. They are even lit in pauses during rain
storms.

The forest country on the hills is also burned at

*233
182 every opportunity. There the purpose is primarily to
232 clear new grazing land. During the 30 months of our
824 major study period, we were in sight of the Mau forest (at the foot of the Mau Escarpment) at least twice a month, often in the rains, and only once did we not see smoke from a fire burning in the trees or brush.

*13 Relations with Wildlife
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The most significant influence the Masai have exerted upon the wildlife is their protection through
[171] excluding hunting tribes from Masailand. The Wanderobo are an exception, but there are relatively so few Wanderobo that they have little effect. The areas of East Africa where the finest assemblages of grassland wildlife still exist are those in Masailand.

224 The animals Masai hunt or have hunted include
[237] buffalo for shields and possibly food, eland for food and
[714] the hides, giraffe for hides and tail hairs (to ornament gourds and dresses,
[531]
[825] according to Millais, 1920), lions and sometimes leopard for defense and for lion manes, and rhinoceros for horns and to spite national park authorities (particularly
*[233] in the past decade). In times of drought the Masai may spear various animals for defense or to avoid competition for scarce water. They will even spear elephants at such times (Grant, 1957).

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224 Masai youths and young Moran may spear any passing animal, possibly to test their skill, but this probably involves relatively few animals in total. It does affect the animals' reactions to the Masai. A Masai driving some livestock, even one cow, is apparently virtually ignored by most wild animals. We watched one Masai drive a lone cow through a herd of 335 wildebeests and 115 zebras. The herd eddied about him at a distance of 20 to 40 yards, and for about a mile he appeared almost a part of the herd, all moving along at about two to three miles per hour. We often saw wild animals grazing in close proximity to Masai livestock and herders. A lone Masai with a spear and no livestock is something else again, and most wildlife will stay nearly 100 yards away from such a person.

857 Masai boys play a game "marking" wild animals. They try to catch young of various species and notch the ears in the same manner as they mark their cattle. Later, when observing the same marked animal they say that it is "my animal." We captured a wildebeest with notched ears in Ngorongoro Crater and a nearby Masai said that it was his wildebeest as he had cut the animal's ears when it was a calf.

232
825 As noted above Masai try to avoid wildebeests

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825 when they are calving because of the snotsiekte disease. In times of drought they try to drive wild animals away from their water holes. When not in use, these holes are often fenced off with a thorn boma to keep them from the wild animals.

#13 Beyond indirect protection, the greatest ecological influence exerted by Masai on wildlife is through their burning and their livestock. The effects of these processes will be discussed below.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai
Wanderobo FL6

OTHER TRIBES

Wanderobo

105 The Wanderobo are a hunting, gathering, and occasionally pastoral people who occupy much of Western Masailand in very small numbers. They and the Masai are traditional allies. As such they are the only people whom the Masai have allowed to live in peace within their lands. Fosbrooke (1948) and others have attributed this to the aid given to the starving Masai by the Wanderobo during the 1890 famine.

Traditionally the Wanderobo are people of small stature who live in wooded country, hunting game and collecting honey. Johnson (1929) records Wanderobo hunters following the migrating herds of wildebeests on the western Serengeti Plain shooting them with poisoned arrows. They took the tails to sell to the Kavirondo tribe who lived near Lake Victoria. Roosevelt (1910) spoke of their hunting and of their living in caves. The German map of the northern Tanganyika portion of Western Masailand (German East Africa Series, Ikoma, 1916) notes "Wanderobo," "Wanderobo kraal" or "Wanderobo settlement" at various points between the Serengeti Plain and the present Kenya border.

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At present the Wanderobo dress and look very much like Masai. Many have married Masai wives and they have bomas much like those of the Masai. We could get no estimate of the numbers of Wanderobo in Western Masailand, but there must be very few not now associated with the Masai.

Most of their hunting is limi[illegible]ccasional antelope for food. Their primary impact on the landscape is through burning. The Wanderobo collect honey from wild hives, often being led to them by the Honey Guide Bird. They also keep hives (Fig. 26). To get at the honey without being too badly stung the Wanderobo build a smokey fire beneath the hive. After they have obtained the honey apparently they do not pay much attention to extinguishing the blaze. Many fires starting in the bush or wooded areas unoccupied by the Masai appear to be started in this way.

A more complete account of the Wanderobo in Masailand is given in a special issue of Tanganyika Notes and Records (Maguire, 1948).

Peripheral Tribes

o6a A series of tribes surround Western Masailand.

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Figure 26.

Bee hives. These are normally made of a cylinder of bark wired or tied in position with enclosed ends. To get the honey the Africans light a smokey fire underneath which drives off most of the bees.

Their contact with Masailand is through some poaching, livestock trading or raiding, and some other forms of trade or commerce. They are all basically agricultural tribes, most of whom also raise a few livestock. Settlement is so dense that they are effective barriers to movement of most animals between Masailand and the other tribal lands.

The Kipsigis tribe adjoins Masailand to the north. Kuria, Ngruimi and Ikoma are to the west in the area north of the Grumeti River and south of Kenya. Near Lake Victoria there are the Bakwaya-Bajita and allied tribes. All along the south from Lake Victoria to Lake Eyasi are the Sukuma who are treated in great detail in the book by Malcolm (1953). The Mbulu (or Iraqw) are south of the Ngorongoro Highlands. Various other sections of the Masai adjoin Western Masailand on the east and above the Siria Escarpment in the northwest.

#13 These peripheral peoples influence the ecology of Western Masailand through burning, poaching, and providing an ecological boundary line. The fires they light for their own purposes within their own tribal areas often carry on into Masailand. Some fires are lit around the edges of Masailand to lure the wildlife out of protected areas so they can be poached. As

*13 noted below, the location and timing of grass fires strongly affects the movements of some of the wild animals.

*** At present, due to adequate protection of game in the Serengeti National Park, most poaching in the Tanganyika portion of the region is outside of the park. For many years Major Temple-Boreham has kept the Kenya side free from any significant poaching. However, in the areas surrounding the park in Tanganyika, especially to the north and west, some poaching does occur. This is in the form of killing by poisoned arrows, rifles, game pits, and snare lines. The latter are the most efficient, and have been found in lines up to five miles long.

*136 Estimates of the magnitude of poaching loss have varied considerably. In 1957 the Kenya Wild Life Society (1957:106) estimated that the annual kill by poachers around the Serengeti National Park "cannot be less than 150,000" animals. Darling (1959) estimated that 100 to 200 animals a week were poached during the periods that the animals were in the Lamai Wedge, immediately south of the Mara area and west of the Serengeti National Park in Tanganyika. In 1959 the Serengeti National Park personnel confiscated 900 steel snares, and in three days in 1957 they took 1,036 snares

136 (Tanganyika Natl. Parks, 1960).

An indirect approach to determine the magnitude of the poaching loss is to compare the known turnover and replacement in the wildlife populations with the known losses. Wildebeests are commonly considered to be the chief sufferers of poaching. In the case of the wildebeests, about eight per cent of the adult population are lost each year (Talbot and Talbot, 1963b). This figure is only some 2,700 animals above the minimum estimated predator kill, which would indicate that the poachers' take of adult wildebeests cannot at present be very great. In the past, however, it may have been very much greater, and the apparent low poacher kill at present must in large part be due to the work of the Park and Game Department personnel.

The Sonjo

The Sonjo are a small tribe living within Western Masailand in a small area southeast of Loliondo. As noted above they were one of the tribes whom the Masai displaced in the mid 1800's.

They cultivate small plots, keep bees, and raise some livestock. Some of their houses are built with a thatch construction rather than with the mud method of

19: Talbot E-4,5 (1956-1962)1964 FL12 Masai FL12

*** the Masai. Griffiths (1940) gives a more complete description of the Sonjo and their history.

49-8 Squatters

In parts of Western Masailand where cultivation is possible, especially on the higher slopes, squatters from other tribes are moving in and establishing small
[582] *shambas* or cultivated fields. The Masai take some of their wives from surrounding tribes. Most of the squatters are relatives of these wives and are therefore allowed to stay by the Masai. The problem is particularly acute in the Mau forest region, where most of the squatters are Kikuyu."

*13 Some cultivation could be carried on in appropriate places with no detrimental effect to the lower plains. However, the system as now practiced results in considerable erosion and substantial vegetation clearance through cutting and burning. Such cultivation, especially in the Mau area, is carried out in the lower margins of the forests which are sub-marginal for cultivation. During the high rainfall years the squatters move in, clear and farm. Two or three years later a dry year forces them to abandon the area. Rainfall is low enough that regrowth is slow while erosion is considerable.

19: Talbot E-4,5 (1956-1962)1964 FL12 Masai FL12

*13 During an 18 month period in 1959 and 1960, the area cleared in connection with dry forest cultivation near Gidanga (east of Narok) increased several hundred per cent.

EUROPEANS

* * *

European is the term used in East Africa to describe any white person, regardless of the country of his origin. Consequently I am using the term in that sense in this paper.

Ancient History

The first European to visit Masailand may have been a Greek merchant named Diogenes in the middle of the first century A.D. According to the Syrian geographer Marinus of Tyre, Diogenes was returning home from a visit to India and landed on the African mainland at a place called Rhapta, possibly the present Pangani north of Zanzibar on the Tanganyika coast (Moorehead, 1962). According to Marinus Diogenes said he traveled inland "for 25 days journey and arrived in the vicinity of two great lakes, and the snowy range of mountains whence the Nile draws its twin sources."(Ibid.). On the basis of this report Ptolemy produced his famous map in the second century A.D. showing the Nile originating from twin great lakes on the equator, which in turn were watered by the Mountains of the Moon (Ptolemy, 1932). If Diogenes saw snow capped mountains and Lake Victoria he must have passed through part of what is now Masailand. The Masai, however, had not yet arrived.

1848-1900

In 1848 the German missionary Johann Rebmann traveled from Mombasa on the Indian Ocean Coast to Mt. Kilimanjaro, discovering it for the modern world. Subsequently a series of explorers traveled the African coast and crossed central Tanganyika. It was not until the 1880's, however, that Masailand itself was entered.

In 1882 the German naturalist G.A. Fischer reached the Rift Valley and discovered Lake Naivasha, which appears on Figure 3 (Roosevelt, 1910). Joseph Thomson crossed Eastern Masailand in 1883 and 1884 and was the first European to bring back a good first hand description of the Masai (Thomson, 1885). In 1899 the German geologist A. Dantz traveled from Mwanza on Lake Victoria through Ikoma (Fig. 3) to the Serengeti Plains (Dantz, 1901). Stuhlman in 1892 crossed the southern part of Eastern Masailand and Baumann was apparently the first European to cross completely the southern part of Western Masailand. He visited Ngorongoro Crater and Highlands and proceeded across the Serengeti Plain and westward to Lake Victoria in 1892 and 1893 (Baumann, 1894).

Also in 1893 Oscar Neumann, a German naturalist, traveled up the Rift Valley, entered Western Masailand somewhere near Narok, and crossed the Loita Plain en route to Lake Victoria (Neumann, 1900).

By 1891 the topography of much of East Africa was known in a general way but there were still many areas that were largely blank on the maps. Western Masailand was one of them (Kiepert, 1891).

1900-1945

In 1906 and 1907 Jaeger (1911, 1913) carried out a most complete exploration and mapping of most of Western Masailand. However, the Kenya portion of Western Masailand still remained blank on his map (1913) and on the subsequent British Ordnance Map (German East Africa Series, Ikoma, 1916).

Kilimafeza Mine (which appears as Kilimaja Nyuka on the German maps)was examined by the geologist Kuntz between 1906 and 1908, for the African Central Mining Company (Kuntz, 1909). Subsequently that mine and others in the vicinity were developed and they have gone through a series of owners (Stockley, 1936). Kilimafeza is still being worked. It is several miles east of Banagi (Fig. 2).

D-8

The Germans surveyed carefully and well what is now the Kenya-Tanganyika border and another parallel belt about 30 to 40 miles south. Much of the area between was not so critically mapped. They established a line of military posts along this southern belt. In Western Masailand these included Ikoma (Fig. 3); Sonjo, about 35 miles southeast of Loliondo; and Olgoss, which is roughly on the present eastern border of the Serengeti National Park in a direct line between Ikoma and Loliondo. After the 1914-18 war these posts were abandoned.

Around 1906-1908 the Siedentopf brothers built two farms in the Ngorongoro Crater. Ruins of some of their buildings are still visible. They apparently attempted some cultivation, raised cattle, and harvested wildebeests. In August, 1960, we were told by Mr. A. Black, an old elephant hunter and scout in East Africa before the first world war, that the Siedentopfs annually took an ox wagon full of wildebeest tails across the Serengeti to sell them to the Kavirondo tribe. The Siedentopfs also provided meat for the German army during part of the 1914-1918 war (Jessen, 1928), and they may have raised some ostriches (Grzimek and Grzimek, 1960).

After the war the German titles were invalidated. In 1921 Sir Charles Ross purchased the title to, or a lease on 16,309 acres of the Crater to preserve the game and provide himself with a winter home. He never was able to be in residence, however, and there was a long litigation between him and the Tanganyika Government which ended by their repossessing the land when the said lease expired in 1940. Apparently a Captain G.H.R. Hurst also had a farm in the crater "for several years" after the war (Joelson, 1928).

There were a few European ranches along the north edge of Western Masailand in Kenya prior to 1911. At least one of these was owned by a Major Carnegie in the Lemek Valley north-east of Aitong (Kenya Game Dept., 648 1911). All European lands in Western Masailand in Kenya were given to the Masai as a result of the treaty of 1911.

[777] At Narok, Loliondo, and Ngorongoro Crater there are District Administration offices and missions. [371] Being a District Headquarters Narok also has a Masai [758] school and hospital. Periodically Europeans, especially [439] South Africans, have run small stores here and there in the area. We were told that one was at Guaso Nyiro,

648 near Narok, and another at Barkitabu on the northwest side of the Loita Plateau.

000 Professional hunting, or "white hunting" as it is known in East Africa, was becoming an important business even before Roosevelt's trip in 1909 (Roosevelt, #136 1910). The Mara area in Kenya was known as an outstanding area for hunting, especially for lions, early in the 1900's (Kenya Game Dept., 1909). In the 1909-1910 Annual Report, the Kenya Game Warden states,"There seems little doubt that the Loita Plains have been very heavily shot over and that game is now very scarce." He recommended closing the area to hunting for eight to twelve months. Again in the next year's Annual Report he noted that the Loita area was the "most shot over" part of Kenya, and he observed that animals, rhinos for example, were changing their habits and taking to bush because of heavy shooting.

During the 1914-18 war sport hunting stopped, but meat hunting was intensified. The Kenya Game Department (1920) estimated that at least 30,000 head of game were taken to feed the troops during the war. These animals came from the Southern Reserve which is essentially Eastern Masailand in Kenya. Because it was so remote,

*/36 Kenya's Western Masailand was not much affected by this activity.

In 1920 a Game Warden was posted to Narok District. His headquarters was Kijabe on the eastern edge of the Rift east of Mt. Suswa. One of his projects was a zebra harvest. He collected over 1,000 the first year for hides (Kenya Game Dept., 1920). Starting in 1928 in Tanganyika a series of game reserves was established, affording various areas different degrees of protection from European ingress and hunting. Between the wars white hunters with their clients visited Western Masailand regularly.

Periodically the Game Warden became worried about the activities of the hunters. In the Annual Report of 1930, for example, he noted that the Mara area was much shot over and that there were always four to five parties hunting. The game was wild, camps with tin cans were littered about, and lions were comparatively rare. At the same time he noted that the herds of plains game, zebra, wildebeest, Thomson's and Grant's gazelles, eland and topi "are larger today than I have ever seen them before." Game laws and their administration were periodically made more stringent.

136 Consequently, since the visiting hunters camped and were continually moving in and out, and since there were limits to the amount of game they could shoot, they made relatively little impression on the landscape or wildlife. There was some meat hunting but apparently not enough to appreciably affect the wildlife.

In the 1920's an American professional hunter, Klein, found a route passable in the dry season by automobile leading from Narok south to Seronera. Since this trip often required several days he set up a semi-permanent camp near the headwaters of the Bologonja River (Fig. 3). Later to help his supply problem he planted gardens there in the care of his African workers. Klein's Camp was abandoned in the early 1930's when Klein died but the area still bears his name. Outside of the mines noted above, Klein's Camp was the only semi-permanent European settlement in the center of Western Masailand.

During the 1930's the Tanganyika Game Department assigned a Game Ranger, M.J. Moore, to look after the Serengeti Game Reserve. A house was built at Banagi and he lived there with his wife until about 1940 (Moore, 1938).

*136 1940-1962

During the second world war there was a wholesale destruction of wildlife in much of Kenya allegedly in the interests of the war effort. Game was shot for a variety of reasons including feeding Italian prisoners of war and protecting ill-considered emergency grain-growing schemes. Simon (1962) gives a graphic description of this period. Thousands of head of zebra and some wildebeest were shot on the Loita Plain during that period. Following the war the Mara area was invaded by biltong hunters. These were residents, mostly of South African origin, who drove trucks into the Mara, set up hunting camps, and shot hundreds of animals. They dried the meat to make biltong (jerky) which they took back to their farms for a meat supply. This was a semi-private form of market hunting which undoubtedly greatly affected the wildlife. In 1950 alone, for example, there was an estimated kill of over 3,500 large animals for biltong.

In the Tanganyika portion of Western Masailand the situation was somewhat different since the area was so remote. There was heavy hunting near Lake Victoria and near the Kenya border, but it does not appear to have approached that of the Mara for intensity. From 1951 to the present much of the area was administered either

*136 as a national park or conservation area, as detailed above.

In 1946 Major E.W. Temple-Boreham was appointed Game Warden of Narok District. He knew the area having worked there before the war when he was in the Veterinary Department. He moved his headquarters to Narok to be closer to the center of the game area, then set about managing the district. During his first two years in office, a total of 292 lions were shot legally in Narok District. By 1948 he had gotten the Kenya game laws changed and totally protected the lions in the center of his district. By 1951 he stopped the biltong hunting. Under his direction, part of the area was declared a photographic reserve, completely protected from hunting. The rest was broken into hunting blocks where only one party at a time could hunt, and where there were strict limits on the number of animals that could be killed. Almost single handedly he effected the first large scale wildlife management project in East Africa. As a direct result the northern part of Western Masailand is by far the finest wildlife area in Kenya.

The Mau Mau terrorist movement came into the open during 1952 and a state of emergency was declared on 21st October of that year. Entry into Narok District was very much restricted as was entry into northern Tanganyika near the Kenya Narok District border. This action brought to a stop hunting and photographic trips into the area, and for about five years the northern part of Western Masailand was very little visited by any Europeans, except during occasional military operations. Being remote and having a good supply of water and abundent game, the area was used as a final retreat by some of the Mau Mau terrorists. The last "general" and what was left of his gang were killed or captured in the center of the study area after we arrived. The best historical account of the Mau Mau and the events leading up to it is by Corfield (1960).

After the formal end of the Mau Mau the district was re-opened to authorized but limited entry. Most of Western Masailand in the District was closed to shooting but could be visited by occasional photographic parties. Hunting was allowed on the Loita Plain and in part of the Loita Plateau.

In 1961 part of the area was set aside as the Masai Mara Game Reserve, as described above.

Veterinary Services 118-1962

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From the end d the 1914-18 war to the present the Departments of Veurinary Services in both Kenya and Tanganyika have ben very active in Masailand. The visible results of thir work involve provision of water supplies, treatment ad prevention of disease, and provision of some exprimental or demonstration ranches whose aim is to encouage better livestock management on the part of the Masai. European veterinary personnel with African assistans have been active in Western Masailand in both Kenya an Tanganyika, and they have exerted a very significant inluence on the ecology of the area. As noted abovetheir work has greatly aided the increase in the numbes of the Masai livestock, without showing any demonstrale improvement in the quality of the livestock, andwith very demonstrable deterioration of the grazing land, specially in the vicinity of the water points.

The significat exceptions are the activities of the Tsetse Survey ad Control Branch of the Kenya Department of Veterinary Services. In Narok District they have maintained wo small field houses (one has since been removed), field laboratory, and an experimental ranch. Their research has been aimed at learning the

648 ecology of the tsetse flies in order to effect their
654
177 control without employing destructive game killing or
232 land clearing schemes (Langridge, 1960, 1961). Within
Western Masailand their work has largely consisted
of careful research and controlled experimentation.

The damage to rangeland resulting from the activities of the other branches of the Veterinary Services are the natural result of a well intentioned, efficient, but narrow approach to the livestock problems of the Masai. Such effects are not limited to East Africa. There are many such examples in the western United States.

ASIANS

●●● Indians were brought to East Africa in the 1890's and early 1900's to help build the Uganda railway. When the railway was completed many of the Indians elected to stay. Many were hard working and industrious. There were willing to work for less than the Europeans, yet were far more skilled and industrious than the Africans. Consequently they prospered. They now own most of the retail and wholesale business and much of the business real estate in East Africa.

In Western Masailand they have accompanied most of the European mining, administrative and business activities. Their most prominent role is that of duka keeper. Virtually all the retail trade goods that enter Western Masailand are handled by the Asian duka keepers. They, with some Somali traders, handle hides and skins buying, itinerant business from trucks visiting the larger bomas, and the trade at dukas at Loliondo, Narok, Ikoma, and Ngorongoro, as well as at a number of small isolated dukas. 439

●●● As a rule they do not herd or hunt or cultivate on more than a back-yard scale. They apparently encourage some rhino poaching, and they sell the wire used for poachers' snares. But aside from that, their ecological importance is indirect. They supply the needs of the peoples who exert direct ecological influences.

TSETSE FLY

#136

The tsetse fly is the most ecologically significant parasite in the study area. The distribution of the fly has determined the distribution of Masai livestock, and this in turn has determined the distribution of overgrazing-devastated lands. Within Western Masailand, the only areas that do not show overgrazing are areas ungrazed (at least recently) by Masai livestock.

The standard reference works on tsetse flies are Buxton (1955) and Swynnerton (1936). The booklet on tsetse flies by the East African Tsetse and Trypanosomiasis Research and Reclamation Organization (1955) is also a good general introduction. The following brief discussion is drawn from these references as well as field data.

The tsetse fly is an arthropod of the genus _Glossina_. In the study area the most common species is _G. swynnertoni_. _G. pallidipes_ is also common in the northern part of the area, and there are several small islands of _G. brevipalpis_ in the west.

Tsetse flies feed on blood, and the period between feedings varies depending on external temperature

*126 and the species of fly. It can vary from a few days to several weeks. When feeding, the fly may ingest trypanosomes from the blood of the host animal. Trypanosomes complete their life cycle inside the tsetse fly and after a varying period, usually about three weeks, the fly can infect another host animal while feeding [69] upon it. One trypanosome causes sleeping sickness in man and another the nagana disease in cattle and some other ungulates.

[169] Human sleeping sickness was formerly relatively common in the area from Ikoma and Banagi westwards. It has not been much problem since the late 1920's, presumably because the human cases have received treatment so that there are few infected host humans for the flies to bite. Nagana disease is common throughout the study area wherever there are tsetse flies. The cattle in the area are generally quite susceptible to nagana, while goats and sheep are highly resistant. The susceptibility of various species of wild animals varies greatly from species to species, but most of the common wild ungulates are not affected, although some may serve as reservoirs for the trypanosomes.

Tsetse flies are quite specific in their host preferences. Langridge ([illegible]) and Lamprey, et. al.

*136 (1962) have shown that the abundance of potential host animals has very little to do with what the flies choose to feed on. In the study area, for example, Langridge (op.cit.) has shown that even where antelopes and zebras make up the greater percentage of the available host animals, they only provide about one per cent of the actual feeds of the tsetse flies in the neighborhood. The flies seek out several less conspicuous and less abundant animals including wart hog, waterbuck and rhinoceros.

Unlike most insects the tsetse flies do not lay eggs. The female produces a single larva at a time. It feeds on milk glands in the body of its mother. When it grows to about the weight of its mother, it is laid in a shady spot. When dropped, the larva usually burrows below the soil surface in humus or loose soil. It then pupates and remains there from about three to ten weeks, depending on the conditions. Then the adult emerges.

The flies are very sensitive to heat, light, and desiccation. They find food by sight and sometimes by scent. Their range of vision is about two hundred yards and within that range a hungry tsetse fly will

*136 follow any moving object. Normally at least three habitats are required for the tsetse flies: breeding spots, resting spots, and feeding spots. Because of these requirements tsetse flies are specific in their habitats and sensitive to habitat change.

Glossina brevipalpis is found in fairly thick vegetation, usually in the vicinity of water, and below 4,000 or 4,500 feet elevation. Therefore the only suitable habitats for it are in the west near Lake Victoria. *G. swynnertoni* and *G. pallidipes* are both tsetses of more arid lands, and both are found to elevations of 6,000 feet. Although there are some differences in their requirements, they are close enough that for this discussion they will be considered together.

All three species of fly can carry both the human and animal trypanosomes. Since *G. brevipalpis* is so limited in distribution it will not be considered here.

For breeding these flies require shady spots with adequate duff or humus on the ground surface. Normally these areas are provided at the base of larger bushes or trees that are shaded or where larger fallen logs or limbs. Heavy grazing affects the ground surface and burning can remove the bush, tree, or fallen wood and destroy the surface humus, exposing the pupae to the

*136 process.

The resting perches of these flies are on the under or shady side of rough barked trees or bushes. These habitats also are removed by hot fires. Thus, changing vegetation from woodland or thickets to a light, open bush will not necessarily kill all tsetse flies immediately but it will reduce the available fly habitats and may render it almost impossible for the flies to reproduce.

Complete removal of the flies might entail complete clearance of all brush, but since the effective vision of the flies is about two hundred yards, an opening about twice that distance across will stop

*136 most flies. Livestock can be grazed relatively safely
231 to within about two hundred yards of fly infested bush.

Where burning is frequent and fairly hot, the fly habitat is impaired. Early, light burns may have very little effect on the flies, and by allowing spread of bush, they may spread the fly habitat. Protection from burning allows spread and thickening of

*136 bush and therefore expansion of fly habitat. The action of elephants pushing down trees and pulling off large limbs

136 provides additional breeding cover for the flies.

The tsetse flies in East and Central Africa have increased their distribution with startling rapidity in the past half century or so. Swynnerton (1936) gives many examples of the speed with which flies were then taking over new country. Even in pre-German days, as noted above, the Masai lost considerable areas of Western Masailand and the land south of the Ngorongoro Highlands to tsetse flies. The reason for this spread, it seems clear, is human land use.

The tsetse flies involved do not survive in dense evergreen thickets or close woodlands or forests, nor do they survive on open treeless grasslands. Their habitat is the edge or the in-between. By burning man opened the former thicker vegetation and created edges or in-betweens. Where his grazing was sufficiently light that dry fuel remained, his fires were hot enough to maintain open flyless grassland. As soon as he started burning too frequently for the fuel to collect, or to overgrazed and removed the fuel, the fires could not suppress the woody growth and tsetse habitat developed. Swynnerton outlined this process in 1936, and we have watched it in action in the study area.

#136 Figure 27 shows the distribution of tsetse flies in Western Masailand in 1890, 1915, 1960, and 1962. We have drawn the data from a variety of maps, reports, and other records. Specific points on the lines were determined by direct evidence (references to tsetse fly or lack of them) or indirect evidence (vegetation type and presence of cattle or horses). Open grassland cannot support these tsetse flies, except in so far as the flies can see moving objects in them. So in making the map we assumed open grassland to be fly-free.

The mechanisms of vegetation change will be discussed below. The important thing at this point is just to show what apparently did occur. The movement of the tsetse flies appears to have been a simple reaction to habitat; where the habitat became suitable the tsetse flies entered it; where it was rendered unsuitable they left. Suitability is considered in terms of the requirements outlined above. The period from about 1890 to about 1950 has been one of expansion of fly bush, extremely rapid at first (during the period when the Masai abandoned or were forced out of the country) and it proceeded at a more regular pace thereafter. From about 1950 to the present the fly bush has been receding.

19; Talbot K-4,5 (1956-1962)1964 PL.12 Masai PL.12

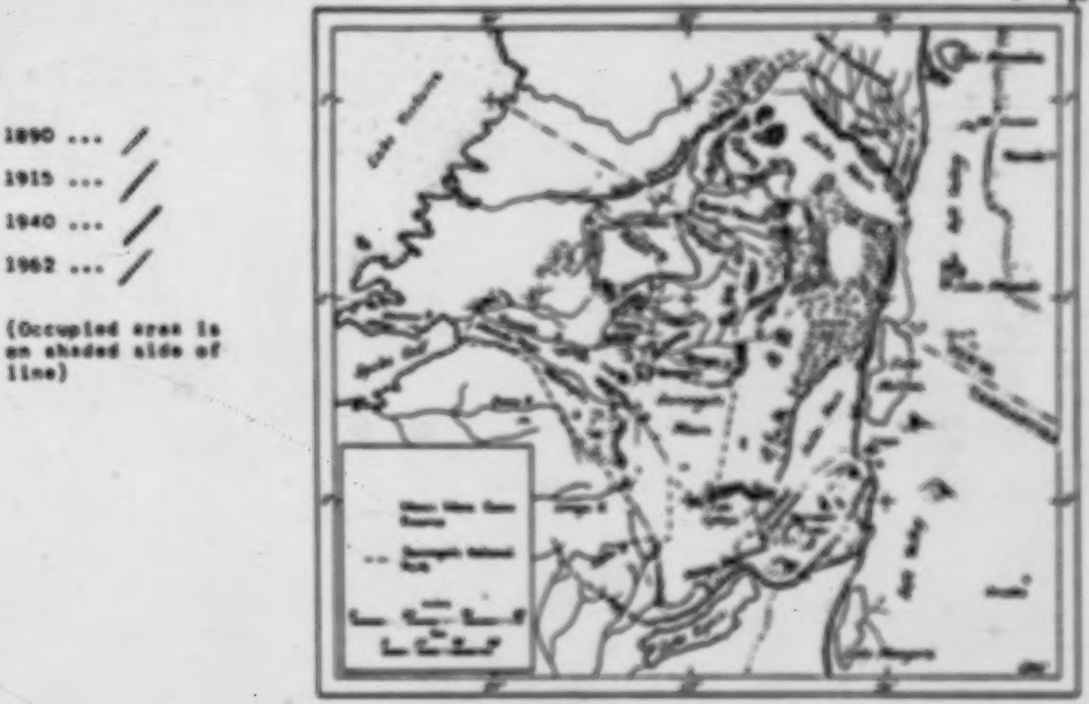
1890 ...
1915 ...
1940 ...
1962 ...
(Occupied area is on shaded side of line)

Figure 27. Approximate Limits of Distribution of Tsetse Flies in Western Masailand, 1890 to 1962.

19: Talbot E-4,5 (1956-1962)1964 FL.12 Masai FL.12

WILDLIFE

12 Scope and Methods

The purpose of this chapter is to describe the role of the wild animals in the grassland ecosystem of Western Masailand. Primary attention is given to the larger ungulates which exert the most direct and obvious influence on the habitat. It is not within the scope of this work to present a detailed life history of each species involved. Instead, I am considering the wild ungulate fauna as a unit component of the grassland ecosystem. As will be shown, the mixed ungulate fauna of Western Masailand can act as an integrated whole, almost as a discrete organism. In my approach to it I am considering it much in that light.

*12.6 Observations. A large amount of information was obtained from observations as described in the chapter on Procedures. The information recorded on the field transect forms (Fig. 7)[6] has provided daily information on life histories, distribution, movements, and population dynamics of all the species found within the area.

[6] [See p. 47.--Analyst.]

Collecting. We obtained detailed information from

*124 examination of over 400 animals representing 18 species. Most of these we shot or captured. The remainder were collected by our cooperators. In addition less complete data were obtained by examination of skeletal remains, mostly skulls, of many more animals.

Animals were collected throughout the year in all habitats and under all conditions available in the region. Collections were arranged whenever possible to coincide with visits of the veterinary personnel so that the animals would yield more data (Fig. 28). Most animals were collected with a single shot placed high in the neck vertebrae. This collapses the animal instantly, with no thrashing or disturbance of other nearby animals, and with no damage to internal organs including the brain. To further minimize the disturbance most animals were shot from relatively long distances, over 300 yards whenever possible. We used a Winchester model 88 lever action rifle in caliber .308, with a variable two and a half to five power telescopic sight, using hard-tipped ammunition. We never wounded and lost an animal.

When shot, each animal was weighed (Talbot and Talbot, 1961, 1962(b)), the temperature taken and standard

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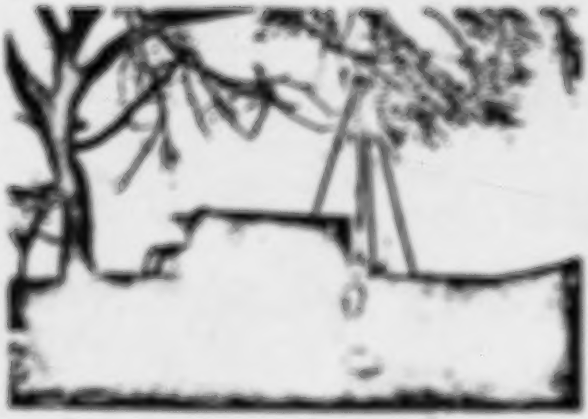

Figure 28.

The East African Agriculture and Forestry Research Organization mobile laboratory set up to carry out carcass analyses on a comparative collection [illegible] in the study area.

*126 standard measurements made (Fig. 29). Body measurements included lengths of head, body, tail, ear (notch to tip), hind foot and hind hoof; heart girth; and shoulder height (backbone to hoof tip, along the curves of the body). Horn measurements included length of outside curve and basal circumference of each horn plus greatest spread and tip to tip distance.

*125 *126 The mouth was examined for tooth condition and for food particles. Ectoparasites were collected when found and notes made of the general condition of the animal and any abnormalities. All data were recorded on the Capture/Kill check sheet (Fig. 30 & 31). The animal was then rolled on its back and the side carved away to expose the organs in situ. Condition of the organs was noted, parasites collected, and the reproductive tract examined and preserved if the condition warranted. Where practical the digestive tract was weighed full and then empty, the weight of the stomach contents being then recorded. A stomach sample was taken and the recently ingested food identified with identification keys we had made, or by direct comparison with the plants growing nearby (Talbot, 1962). If the area was new to us we would make a vegetation plot and a collection of available grasses. All data from the post mortem

[TEXT CONTINUED ON PAGE 202]

*126

Figure 28.

Weighing an immobilized topi. The telescoping derrick is extended to about two thirds of its maximum height. Animals to be weighed are put in the canvas sling and the rings on the attached straps are hooked onto the scales. The animal is then cranked up with the hand winch, visible to the right of the topi's head.

19: Talbot K-4,5 (1956-1962)1964 FL.12 Masai FL.12

Figure 30.

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[illegible]

Figure 31.

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[illegible]

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*126 examinations were recorded on the check sheet for Post Mortem examinations (Fig. 32 and 33) which serves as a companion sheet to the Capture/Kill form (Fig. 30 and 31).

Capture and Marking: Detailed information on behavior and movements of wild animals must come from individuals which can be identified and observed over a period of time. Only rarely did we find an animal with natural markings sufficiently distinctive to identify it from the thousands of other animals in the study area. Consequently we relied on artificially marked animals for data on individual movements and behavior.

We used field immobilization techniques to capture wildebeests and other animals for examination and marking (Fig. 34 and 35). Details of the immobilization drug physiology and technique are presented in papers by Talbot (1960b), Talbot and Lamprey (1961), and Talbot and Talbot (1962a). The immobilized animals were examined, weighed where possible (Fig. 36), food was collected from their mouths, and they were marked and released. Results of the examination, markings, and details of immobilization and drugs were noted on the Capture/Kill form (Fig. 30 and 31).

Figure 32.

[illegible]

Figure 33.

[illegible]

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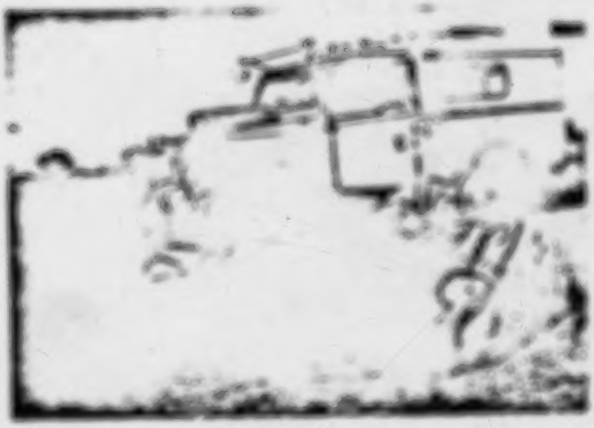

Figure 24.

Lee M. and Martha H. Talbot with an immobilized wildebeest. Note the ear markers on the wildebeest. The safari-equipped Land-Rover is in the background, with extra lights, removable side panels, and ports in roof visible.

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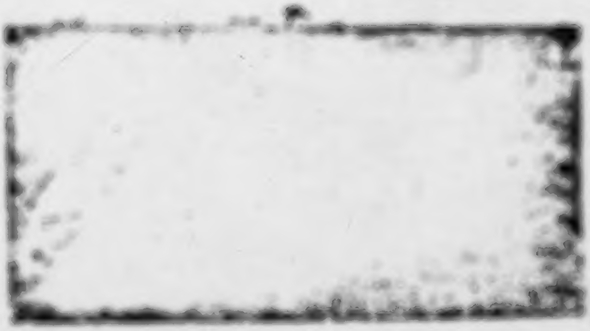

Figure [illegible].

Shooting a rhinoceros with a capture gun. One dart is visible in the animal's side. A Park ranger with a high-powered rifle is backing up the CO_2 powered dart gun.

This area has been protected from fire for about three years and the whistling thorn (*Acacia drepanolobium*) has grown to three to five feet high.

*/15
#/16 We marked the animals by attaching metal or plastic ear tags and colored plastic strips (Fig. 36), by painting horns and occasionally backs, and, in addition for wildebeests, by bobbing tails and beards. By using various color combinations in the plastic ear strips, individual animals could be identified at distances over 100 yards with binoculars. The plastic used was commercial P.V.C., usually in strips about eight inches long and one half inch wide, occasionally in shorter, wider strips. The strips were attached to the ears by rivet-type ear tags or tied through a slit in the ear by a jesse knot (Craighead and Stockstad, 1960). The latter method was found most successful on wildebeests. However, a topi marked with plastic rectangles fixed to the ear by a rivet ear tag still wore its tag when observed in November 1961, over 19 months after marking.

Cutting tail hair and the beard greatly facilitated spotting a marked wildebeest, even in a large herd. In two cases wildebeests lost their ear tags and were initially identified again three and five months later by the pattern of their cut tails.

Paint, both rubber base and plastic base, usually wears off the body in about three weeks and the

TEXT CONTINUED ON PAGE 2[illegible].

19: Talbot E-4,5 (1954-1962)1964 FL12 Manual FL12

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Figure [illegible].

[illegible] P.V.C. plastic [illegible] The [illegible] several [illegible]

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horns in two to six weeks. While the color remains, however, it greatly facilitates finding the animal. In two cases paint-marked wildebeests were located and observed from a small aircraft daily for periods of about two weeks ([illegible] and Talbot, 1961:194-195). They were easily distinguishable from altitudes of about 1,000 feet.

We did not recover any evidence -- painted horns, ear tags, or carcasses -- of fatalities in the marked wildebeests in the Serengeti-Mara Plains region. However, as of December, 1961, the skulls of six marked wildebeests had been recovered from the Ngorongoro Crater where the limited area and daily visitors during the dry season made recovery more likely. Unfortunately four of the six were lost before identification was possible. The two identified were marked by the Tanganyika Game Department. One was apparently killed by a lion two months after marking, about two miles from where it had been released. The other was picked up several months after marking. The six were picked up in an 18 month period after marking. In Kajiado District, a young Masai boy speared one marked wildebeest before it had completely recovered from the drugs.

*125 Determination of numbers and density. We obtained density figures and local censuses from the field techniques as described above, sometimes augmented by counts from prominent view points. However, in a region of 12,000 square miles it is not possible for a ground crew to cover enough area rapidly enough to ensure an accurate regional count. Aerial photo-mosaics of the whole region would provide the most accurate count of animals, at least in open areas, but the cost is prohibitive.

Census methods or indices of ungulate numbers have been determined using pellet counts (Bennett, et. al., 1940; Eberhardt and Van Etten, 1956; Leopold, et. al., 1951; Riney, 1957). However, when we tried to apply these methods to the study area it became obvious that the method was not consistent under the variety of conditions involved. Presumably this is due to a high invertebrate population -- dung beetles (Scarabaeidae), ants, etc., which quickly dispose of or disperse dung piles -- and irregular rainfall. We therefore concentrated on techniques using light aircraft.

*125 *126 During 1959 and 1960 we carried out a cooperative program of aerial wildlife census with Captain D.A.P. Zaphiro of the Kenya Game Department, a pioneer in aerial

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*119 wildlife work in East Africa. The aims of this program were two-fold: to work out methods of efficient, accurate aerial wildlife census and determination of population composition, and in the process, to survey game populations on one large study area. Some of the techniques and results have been presented elsewhere (Talbot and Stewart, 1964; Stewart and Talbot, 1962).

In 1961 this work was augmented by a cooperative project with Mr. D.R.M. Stewart of the Kenya Game Department and Captain R. [illegible] of Wilken Air Services, Nairobi, which culminated in May in an aerial census of the wildebeests and other major species covering the entire 12,000 square miles of wildebeest habitat within the study area, and 3,000 additional square miles around the perimeter to ensure that no fringe populations would be missed. This was a cooperative project with the Fauna Research Unit of the Kenya Game Department, Wilken Air Services, and the Tanganyika National Parks.

*125
*126 The census was carried out between May 18 and May 21, with 77 hours being flown on counting and reconnaissance. The aircraft used were a Piper Tri-Pacer and a Piper Cruiser, high wing monoplanes with good visibility and slow stalling speed (Fig 8). The same

*125 *126 pilot and two observers were used throughout the actual counting. Counting started in the north and moved rapidly south, with our wives and African Game Scouts moving camp from landing area to landing area to reduce the flying time travelling to and from camp. The whole region was divided into areas, and each area subdivided into small counting units with recognizable topographic boundaries such as trails or watercourses. (Fig. 27 and 28b). These units were made as small as possible, usually one to five miles in width. The aircraft was flown back and forth across each unit in parallel tracks, usually at an altitude of 400 to 700 feet (for best visibility without frightening the animals), with the observers counting strips of from 150 to 400 yards on either side of the aircraft (Fig. 27, 28a and 28b).

Groups of animals too large to be counted in one pass (tight groups of over about 25 animals) were circled, and if too concentrated for accurate visual counting, they were photographed with a Leica M-3 35mm camera with 50mm lens, using High Speed Ektachrome at 1/1000th of a second. Thirty-seven per cent (85,278) of the total numbers of wildebeests were counted from these color slides, subsequently projected on a large screen over a counting grid.

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Figure 37.

Aerial wildlife census on the Serengeti Plain. Flying at this altitude, about 700 feet, the animals are clearly in view yet are not disturbed. Drainage lines, trees, and game tracks such as those in the background provide boundaries for counting strips.

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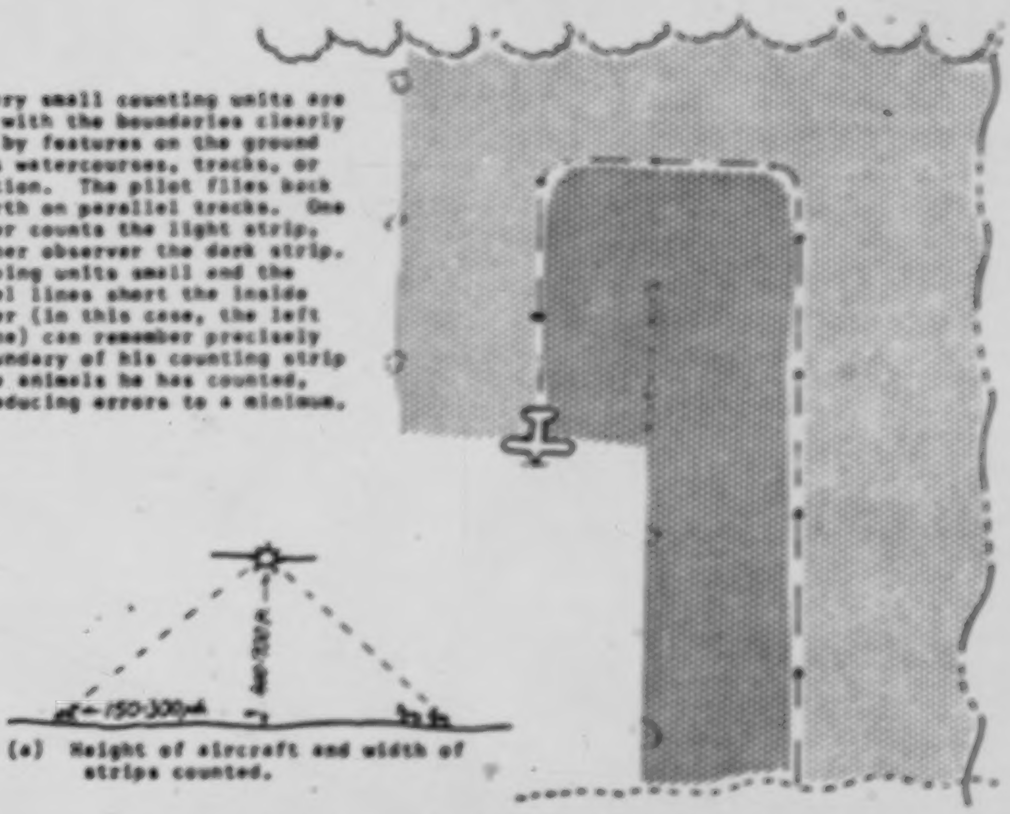

(b) Very small counting units are chosen with the boundaries clearly marked by features on the ground such as watercourses, tracks, or vegetation. The pilot flies back and forth on parallel tracks. One observer counts the light strip, the other observer the dark strip. By keeping units small and the parallel lines short the inside observer (in this case, the left hand one) can remember precisely the boundary of his counting strip and the animals he has counted, thus reducing errors to a minimum.

(a) Height of aircraft and width of strips counted.

Figure 38. Diagram of Aerial Wildlife Census Method.

#125
#126 Hand tally counters were used to keep track of numbers of animals visually counted. Totals were entered on an aerial survey check sheet (Fig. 30). Also entered were other data including location, age, and sex composition where taken and land conditions. Location of all wildebeests counted was plotted on maps. Each day reconnaissance flights were carried out to see if any movement (obvious both from tracks and position of animals) had taken place between counted and uncounted areas. Where such movement had occurred recounts were made. Where counted animals were moving toward uncounted areas, buffer zones ahead of them were counted immediately to ensure that no duplication took place (Stewart and Talbot, 1962a, 1962b).

On May 19th, 1961, a Royal Air Force Canberra photographic reconnaissance aircraft photographed the main concentration of wildebeests on the west edge of the Serengeti Plain. The films were taken to London and a photomosaic made, from which as an exercise in photo-interpretation the R.A.F. personnel counted the
#136 wildebeests. Their total was 194,411 wildebeests. The
#125 day of the R.A.F. photographic flight we were working
#126 on the Serengeti Plain and counted an additional 3,000

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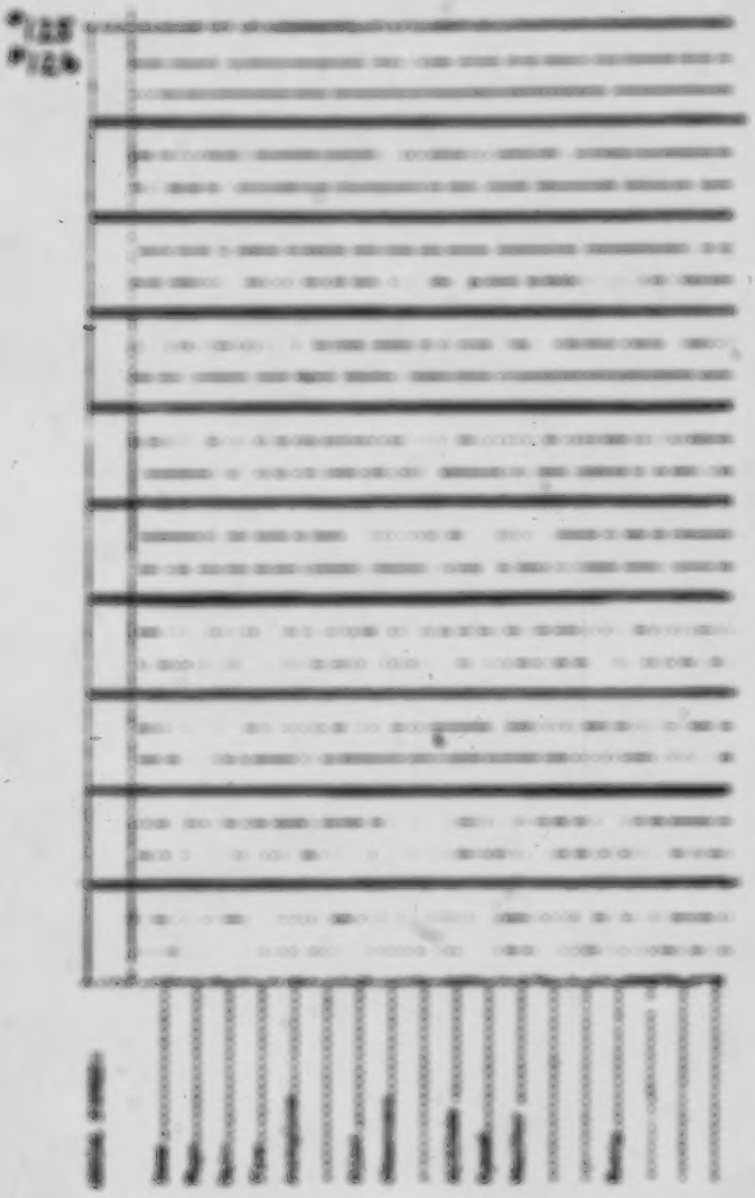

Figure 38. [illegible]

*[15] *[17] *[16] wildebeests not photographed by them on the central plains, plus some additional animals at the edge of the wooded country to the west of the photo count, giving a total actual count that day of 107,411 wildebeests, plus the uncounted animals in the woods.

Seven days later when we made our aerial census of the area our count of the same animals (as evidenced by clearly defined tracks) was 107,000-110,000 animals (we were uncertain whether or not 3,000 of the animals were those that had been previously counted by the R.A.F.). Our lower figure was 0.38 per cent under the R.A.F. count, and our higher figure 2.41 per cent over it. The apparent accuracy of this double count is particularly gratifying because the animals involved in both counts, being concentrated and in difficult terrain, were by far the most difficult wildebeests to count in the whole area. We would, therefore, expect to find our maximum error here.

*[16] We made one count of the wildebeests in the Ngorongoro Crater, using ten-power binoculars from the Crater rim on December 19, 1959. We divided the Crater floor into nine well defined units and counted the animals in each unit. In the nearer six units the count was believed relatively accurate, and we allowed a

conservative 10 per cent margin of error. In the farthest three units distance reduced the probable accuracy. In a few cases other animals might have been mistaken for wildebeests, and some wildebeests may have been hidden by the hills. So we increased the margin of error for these units to 20 per cent.

.24 Species Involved

The common large animals in Western Masailand include the following (nomenclature follows Swynnerton and Hayman, 1950):

Carnivora:

Otocyon megalotis virgatus Miller. Bat-Eared Fox.

Canis mesomelas mcmillani (Heller). Black-Backed Jackal.

Canis adustus notatus (Heller). Side-Striped Jackal.

Lycaon pictus lupinus Thomas. Wild Dog.

Crocuta crocuta (Erxleben). Spotted Hyena.

Acinonyx jubatus (Schreber). Cheetah.

Panthera pardus (Linnaeus). Leopard.

Panthera leo massaica (Neumann). Lion.

Proboscidea:

Loxodonta a. africana (Blumenbach). African Elephant.

12.4 Perissodactyla:

Diceros bicornis (Linnaeus). Black Rhinoceros.

Equus burchelli böhmi Matschie. Zebra.

Artiodactyla:

Aepyceros melampus suara (Matschie). Impala

Alcelaphus buselaphus cokii Günther. Hartebeest or Kongoni.

Damaliscus lunatus jimela (Matschie). Topi

Gazella g. granti Brooke. Grant's Gazelle.

Gazella thomsonii biedermanni (Knottnerus-Meyer). Thomson's Gazelle.

Giraffa camelopardalis tippelskirchi Matschie. Giraffe.

Kobus defassa adolfi-friderici (Matschie). Waterbuck.

Syncerus c. caffer (Sparrman). Buffalo.

Taurotragus oryx pattersonianus Lydekker. Eland.

There are a number of other less common or smaller animals in the study area. The most comprehensive list is given by Swynnerton (1958).

12.5 Weight

Weight is probably the most useful index to comparative size of the ungulates in the study area. Knowledge of the relative sizes of the ungulates provides [illegible] one index -- but by no means the only index -- of the relative significance of the ungulates in the grassland ecosystem. In terms of green forage consumed one elephant is more important than one impala. Biomass is an important measure of the biological productivity of an area, and weight, obviously, is basic to calculations of biomass.

Therefore, to put the various ungulates into the perspective of the ecosystem, it is useful to consider their weights and then their relative abundance.

[illegible] There are very few published records on average weights of East African animals. Much of the few records that exist are from trophy animals and hence are not representative of the population involved. Roosevelt and Heller (1914) and Meinertzhagen (1938) have given some weights but few of these are from the study area. Consequently whenever possible we weighed animals that we or our cooperators killed or captured. To accomplish this we constructed a telescoping derrick with a hand winch on the rear of the Land-Rover (Talbot and Talbot, 1962b). The Kenya Department of Veterinary Services kindly provided us with an accurate certified Salter trade balance which weighed objects up to 1,120 pounds.

#134 #115 An animal's weight does not necessarily rise evenly from birth to adulthood and then remain fixed. There may be seasonal fluctuations as illustrated for deer by Leopold, et. al. (1951) and Taber and Dasmann (1958). The rate of growth may vary from one period to another, and some animals at least, reach a peak adult weight and then gradually lose weight during later life. This effect is shown by our records for the wildebeests in Western Masailand (Fig. 46).

Other factors that influence weight are stomach fill of food and water. Payne (1963) has shown that cattle can lose up to 17 per cent of their body weight after three days without water, then make it up in one watering. The stomach fill of adult male wildebeests averages 66.7 pounds (13.4 per cent of its weight), but the range is from 30 pounds to 83 pounds.

Therefore, since liveweight of any species of animal will fluctuate considerably an average weight must be considered as an arithmetic mean around which the true liveweight fluctuates. However, with wild animals collected at different times of day and at different seasons, the mean of weights of a given age class may come as close as possible to the mean true weight of the species.

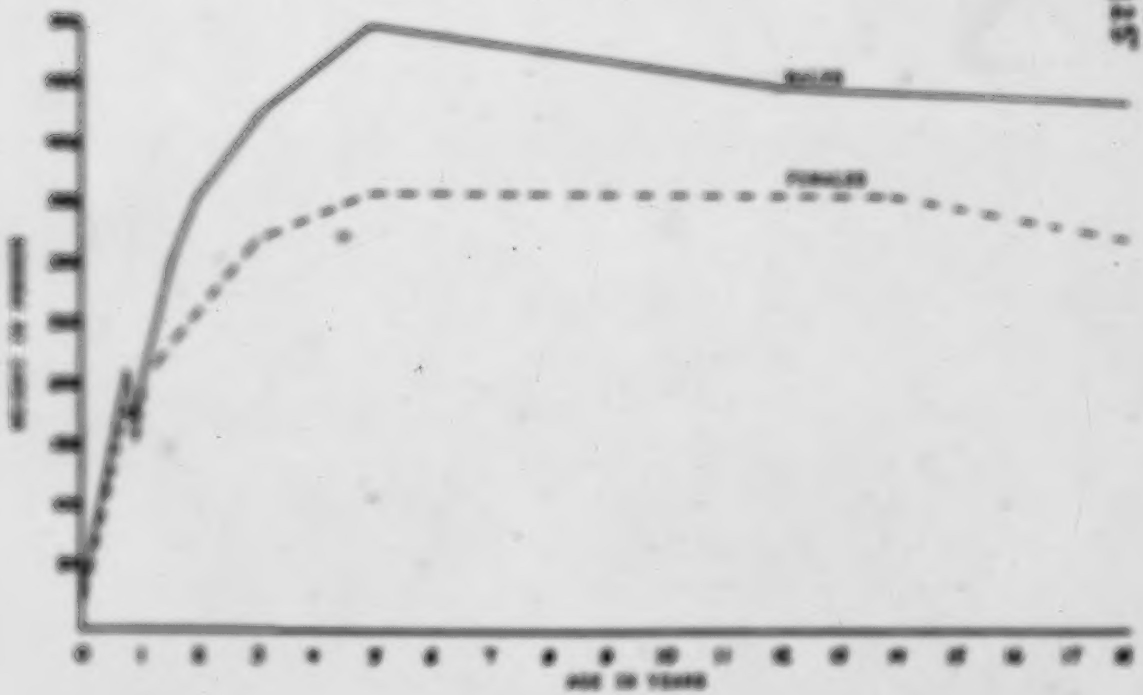

Figure [illegible]. Average Weights of [illegible] by Age-

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[illegible] Talbot E-4.3 (1956-1962)1964 [illegible]

19: Talbot M.-4.5 (1956-1962)1964 F1.12 Masai F1.12

#126

#125 Table 8 gives the average weights of some wild animals in the study area.

#179 **Results**

#125 Population Counts of Wildebeest: It generally
#126 has been assumed that the Serengeti-Mara region contained two separate populations of game, the Tanganyika population centered on the Serengeti Plain, and the Kenya population centered on the Loita Plain. Until very recently, management of these areas was based on this assumption, and the few wildlife estimates or censuses have been carried out either in one area or the other (Brooks, 1961; Darling, 1960; Grzimek and Grzimek, 1960b; Pearsall, 1957; Swynnerton, 1958).

In 1953 Brooks (1961:12) attempted to census the Thomson's gazelles on the central Serengeti Plain. Aside from that, prior to 1958 no organized attempt had been made to determine the wildlife populations in either the Tanganyika or the Kenya portions of the region. Visitors have noted with wonder the impressive Serengeti wildebeest migrations. Martin Johnson (1929:267) for example, wrote of "miles and miles of the wildebeest in herds that must have numbered into the tens of thousands." Pearsall (1957:8,9) made "a very rough estimate" of the numbers of wildebeests, based on

(TEXT CONTINUED ON PAGE 225)

136 Table 8. Average Adult Live-weights of Some Ungulates in Western Masailand

Species	Weight in pounds	
	Females	Males
Thomson's gazelle	[illegible]	[illegible]
Grant's gazelle	[illegible]	[illegible]
Wildebeest	[illegible]	[illegible]
Burchell's zebra	[illegible]	[illegible]
Topi	[illegible]	[illegible]
Kongoni	[illegible]	[illegible]
Impala	[illegible]	[illegible]
Dik dik	[illegible]	[illegible]
Buffalo	[illegible](1)	[illegible](1)
Eland	[illegible]	[illegible](1)
Elephant	[illegible](2)	[illegible](2)
Giraffe	[illegible](1)	[illegible](1)
Black rhinoceros	[illegible](1)	[illegible](1)

(1) Estimated from only a few records.

(2) Estimated from data in Buss, [illegible], and Buss and [illegible], [illegible].

[illegible] observations made from the ground and from flights over a period of about two months (Table 8). Swynnerton (1958:[illegible]) gave a "very approximate" estimate of the numbers of wildebeests in the Serengeti region (Table 8). His estimate was based on ground and aerial observation and sample counts, and on long experience with the area. In 1958 Grzimek and Grzimek (1960b) made an aerial wildlife census of a variety of species in and near the former boundaries of the Serengeti National Park, including what they considered to be the total Serengeti wildebeest population (Table 8).

The first organized count on the Kenya side of the region came in 1958 when a combined aerial and ground census was made in the course of the ecological reconnaissance of that area carried out by Darling (1960b:[illegible]).

Results of the Present Studies. During 1959 and 1960 we and the Kenya Game Department made a series of estimates based on sample counts and full censuses of the wildebeest population on the Kenya side.

These counts had shown that the Kenya wildebeest population had dropped from about 15,000 in 1956 to around 6,000 in 1960 (Table 9, Mara). This drop in [illegible]

(TEXT CONTINUED ON PAGE 227)

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]	[illegible]	[illegible][illegible]	[illegible]	[illegible]
[illegible]	[illegible]			
	[illegible]	[illegible]	—	—
	[illegible]	[illegible]		
	[illegible]	[illegible]	—	—
	[illegible]			
	[illegible]	[illegible]	—	—
	[illegible]			
	[illegible]	—	[illegible]	—
	[illegible]			
	[illegible]		[illegible]	
	[illegible]	—	[illegible]	—
	[illegible]		[illegible]	
	[illegible]	—	[illegible]	—
	[illegible]			
	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]			
	[illegible]	[illegible]	—	—
	[illegible]			
	[illegible]	—	[illegible]	—
	[illegible]			
	[illegible]	—	[illegible]	—
	[illegible]			
	[illegible]	[illegible]	[illegible]	[illegible]

[illegible]

#125 numbers represented far too high a loss to be explained
#126 on the basis of known mortality, and the only explanation was that the loss was due to emigration. We had previously found this to be true by following herds from Tanganyika to Kenya, and back, and by analyzing our daily strip counts. In addition, we had captured and ear-tagged a female topi on 17 July, 1960, in Kenya. In the first week of November, this topi was observed with a young calf at heel at Seronera Camp, about 100 miles south in Tanganyika (Mathews, 1961). Although we did not observe this topi at Seronera, we feel there is little chance for error in the observation for the following reasons: The observer is an experienced professional hunter, well known to us, who is deeply interested in natural history; he and his party observed the animal from close range noting its prominent plastic ear tags and that it was a female with a calf at heel; the only other marked topis in the region at that time were another female from Kenya, and an old, one-eyed, partially lame male from Seronera with different ear tags. The observation is significant in that it is the only marked animal of any species observed to cross the territorial border, and its deduced movements duplicate those observed at the same time of a large concentration of wildebeests.

#124 Our population estimates in Tanganyika during 1959 and 1960 were quite at variance with the count of Grzimek and Grzimek (1960b). In February, 1960, for example, we estimated 150,000 wildebeests visible during a single drive across the Serengeti Plain, while the Grzimeks' total figure for the whole park was only 99,481.

#125 128 It became obvious that a single census of the entire Serengeti-Mara region would be required to determine accurate enough total population figures either for our purposes or for those of the game or parks personnel involved. In May, 1961, as the cooperative project described above, we carried out a complete aerial census of the region. The results of that census, compared with previous figures for the region, are presented in Tables 9, 10, 11, and 12.

#136 b125 (c) Ngorongoro Crater. For reasons of time and finance, Ngorongoro Crater was not counted during the May census. The results of our only count, in December, 1959, as described above, are as follows: nearby units = 4871 wildebeests ± 487 (10 per cent); distant units = 4850 wildebeests ± 970 (20 per cent). The total counted was 9721, with the above possible error allowing a range of 8,264 to 11,178 wildebeests.

19: Talbot E-4,5 (1956-1962)1964 FL12 Masai FL12

Table 10. Cooperative Wildlife Census of Western Masailand, May, 1961.

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The High Visibility Species
With Probable Accuracy of Count to Within 10%,
compared with previous figures for the region.

SPECIES	SOURCE & DATE	SERENGETI(1)	MARA	TOTAL
Topi	Grzimeks, Jan. 1958 aerial census.	5,172	—	—
	Darling, Oct.-Nov. 1958 "estimate from critical sample counts"	—	4,000	—
	Talbot & Stewart, May 1961 possibly 10% low.	15,766	4,111	19,877
Buffalo	Grzimeks, Jan. 1958 aerial census.	1,813	—	—
	Darling, Oct.-Nov. 1958 "estimate from critical sample counts"	—	4,000	—
	Talbot & Stewart, May 1961	15,898	5,934	21,832
Elephant	Grzimeks, Jan. 1958 aerial census.	60	—	—
	Darling, Oct.-Nov. 1958 "estimate from critical sample counts."	—	500	—
	Talbot & Stewart, May 1961	702	455	1,157

Footnote: (1) Excluding Crater Highlands.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

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Table 11. Cooperative Wildlife Census of Western Masailand, May, 1961.

Results of Present Census.

The Low Visibility Species with Partial Counts or Estimates,(1) compared with previous figures for the region.

SPECIES	SOURCE & DATE	SERENGETI	MARA	TOTAL
Kongoni	Grzimeks, Jan. 1958 aerial census.	1,285	—	—
	Darling, Oct.-Nov. 1958 "estimate from critical sample counts."	—	1,000	—
	Talbot & Stewart, May 1961 minimal count, population possibly substantially higher	1,379	721	2,100
Eland	Grzimeks, Jan. 1958 aerial census.	2,452	—	—
	Darling, Oct.-Nov. 1958 "estimate from critical sample counts."	—	500	—
	Talbot & Stewart, May 1961 Partial Count	2,450	750	3,200
	Estimate based on count.	4900-7350	1500-2250	6400-9600
Rhinoceros	Grzimeks, Jan. 1958 aerial census.	11	—	—
	Darling, Oct.-Nov. 1958 "estimate from critical sample counts."	—	100	—
	Talbot & Stewart, May 1961 minimal count, only small proportion of total.	29	54	83
Thomson's gazelle	Pearsall, 1953 estimate from ground sample	180,000	—	—
	Grzimeks, Jan. 1958 aerial census. sample counts	194,654 (3)	—	—
	Darling, Oct.-Nov. 1958 "estimate from critical	—	12,000	—
	Talbot & Stewart, May 1961 rough estimate.			480,000 - 800,000
Lion	Temple-Boreham, Talbot 1961 estimate based on ground counts.	—	200-300	—
	Talbot & Stewart, May 1961 Partial count Rough estimate.	75 300-400	84 250-300	[illegible] 550-700

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Table 12. Cooperative Wildlife Census of Western Masailand, May, 1961.

Results of Age-Group Sample in Census.

SPECIES	NUMBER IN SAMPLE	SAMPLE, PER CENT OF TOTAL COUNT	PER CENT YOUNG IN SAMPLE
Wildebeest	1,604	0.7	18.2
Zebra	1,128	0.7	10.5
Topi	194	1.0	22.2
Kongoni	93	4.4	17.2
Eland	46	1.4	17.4
Rhinoceros	83	100.0	14.4
Elephant	29	2.5	17.2

(Table 12 continued)

Footnotes. (1) C.F. text for basis of estimate.
(2) Excluding Crater Highlands.
(3) Combined figure for Thomson's gazelle and Grant's gazelle; however, Grant's gazelle make up a very small percent of the total gazelle population.

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Other counts and estimates available to us are presented in Table 13. Excluding the Grzimek's count, the mean of the previous figures is 8,864, which is within ± 15 per cent of all figures -- a reasonable allowance for error from counts and estimates in these conditions. This is remarkably close agreement, and would indicate a relatively stable population of roughly 9,000 animals.

The Grzimeks' count is substantially lower, however, according to Grzimek and Grzimek (1960:47-48 and 60-66) their count in the Crater was their first attempt at aerial work, and they noted on its completion that (Ibid, p. 66) "all this would have to be repeated..." to increase reliability. Comparison of the figures they give for the wildlife population of the Crater for their first flight (1960:66) with their final figures 1960a:36-37) shows no change, so apparently they were unable to repeat the flight and therefore accepted their first figures.

(b) Kenya Mara: The counts and estimates of the wildebeests in the Mara region of Western Masailand are presented in Table 14. The differences between these reliable counts (ranging from under 6,000 to about 23,000 illustrate the fluctuations in

[TEXT CONTINUED ON PAGE 235]

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Table 13. Counts and Estimates of the Wildebeest Population of the Ngorongoro Crater.

Source	Date	Numbers
Pearsall (1957) estimate	Nov. - Dec., 1956	10,000
Swynnerton (1957) estimate	1946 and before	8,000 - 10,000
Grzimek and Grzimek (1960; 1960a) aerial census	Jan., 1958	5,360
Molloy and Harvey, estimate (Grzimek and Grzimek, 1960a)	March, 1959	7,800
Talbots, count from rim	Dec., 1959	9,721 ± 1,450
Moore-Gilbert, count in Crater	Sept., 1961	7,800

Table 14. Counts of the Wildebeest Population in the Kenya Mara.

Source	Date	Numbers
Darling (1960) census	Oct. - Nov., 1958	15,000
Talbots, periodic aerial and ground sample counts	Nov, 1959- Nov,1960	6,000 - 8,000
Zaphiro (1960) and Talbots	Feb., 1960 & July, 1960	about 6,000
Grimwood (1960) aerial count	April, 1960	5,897
Stewart and Talbot (1962a, 1962b) aerial count	May, 1961	17,817
Stewart and Zaphiro (Kenya Game Dept., 1962)	Oct., 1961	22,916

*136 population due to movement into and out of Tanganyika.

Table 15 compares the counts and estimates of the important ungulates other than wildebeests, in the Kenya Mara. From these figures it is clear that zebra, topi, buffalo, elephant, and eland are markedly migratory.

Conclusions: The population of ungulates counted in May, 1961, totalled between 943,000 and 1,266,000 animals. In addition there is a high population of impalas, a significant number of Grant's gazelles and giraffes, some roan antelopes, hippos, and wart hogs, and numerous smaller antelopes including duikers, steinboks, dik diks, reedbucks and oribis.

Between a half and a third of the ungulates counted were wildebeests and zebras. They are, therefore, the most important ungulate species in terms of biomass. The wildebeests are the most important single species from that standpoint.

Another estimated half to two-thirds of the total numbers were the little Thomson's gazelles. Although numerous, because of their small size they provide much less biomass.

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Table 15. Counts of Various Wild Ungulates in the Kenya Mara.

Source	Date of count	Numbers					
		Zebra	Topi	Buffalo	Elephant	Kongoni	Eland
Darling (1960)	October-November, 1958	12,000	4,000	4,000	500	1,000	500
Grimwood (1960)	April, 1960	7,000					
Talbot & Stewart	May, 1961	20,867	4,111+	5,934+	455+	721*	750**
Kenya Game Dept. (1962)	October, 1961	13,595	2,680	4,163	143	821	173

+ Probable accuracy within about 10 per cent, believed a low count.

* Minimal count, population possibly substantially higher.

** Partial count estimated total 1,500 to 2,250.

*126 Ungulate Food Habits

Methods: Initially we made an attempt to determine the foods eaten by wildebeests and other plains animals by observation alone. The results were not satisfactory. Where up to forty different grasses can be found on one hillside, and over twenty species of herbivores feed on them, it is virtually impossible to determine through observation alone which animal is eating what grass. Accordingly we have based our determinations of food habits on examination of the stomach contents of the various animals that we collected and on food found in the mouths of immobilized animals.

The rumen and reticulum of freshly killed animals were opened and the contents spread out evenly. Recognizable items were then identified, either using keys we had constructed, or by comparison with plants growing in the area. In the latter case vegetation samples were collected for the East African Herbarium to check identification. The component items were then segregated, and estimates were made of the relative volume of green material to dry, and grass to other types of food.

To determine the relative quantities of each

*126 food eaten we used two methods:

*126 1. A grab sample was taken and the percentage *125 occurrence of recognizable items in it was determined by counting the items (Talbot, 1962). The sample was then preserved.

2. After initial identification of the different food plants in the stomach contents, the relative volumes of each item were estimated.

In addition we have carried out cooperative food habits studies with Dr. and Mrs. D.R.M. Stewart of the Fauna Research Unit of the Kenya Game Department. They have developed a method to identify plant remains in stomach samples or faeces through microscopic identification of fragments of cuticle from the plant leaves (Stewart and Stewart, 1962). We have given the Stewarts our collection of rumen samples with notes on grass species found in the vicinity of collection. This has provided the Stewarts with a mass of organized material for laboratory study and provided us a most valuable check and confirmation on our field identification methods.

To establish what foods were available to the animals whose stomach contents we identified we made vegetation plots on the sites where the animals had been

*125 observed feeding when shot. These are described below *126 in the chapter on Vegetation. Wherever possible individuals of several different species of ungulate were collected at the same time in the same place, so that any differences between their stomach contents would represent choice rather than local differences in available foods. This type of collecting was possible because animals hit in the neck vertebrae collapse quietly, normally without even kicking, and without frightening other animals grazing beside them. When shot from long range (300 to 400 yards) the sound of the shot did not disturb the animals either. Consequently we occasionally dropped three or four different animals that were almost touching each other.

Food Habits: Our most complete data on food habits come from wildebeests, and the microscopic checks of the Stewarts have been made on that species. Therefore we shall consider the wildebeest first.

*136 *125 (a) Wildebeests: Tables 16 and 17 present the results of the three methods of stomach contents analysis. Assuming equal accuracy in identifications, it would be expected that estimates of volume of food items in the entire stomach (Table 16, Column 1) should more closely reflect the actual amounts of food ingested than

[TEXT CONTINUED ON PAGE 243]

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Table 16. Results of Three Methods of Analysis of the Stomach(1) Contents of Western White-Bearded Wildebeests(2)

Food Item(3)	Macroscopic Identification(4)		Microscopic Identification(5)
	Volume - Est. % of Total Contents of 149 Stomachs	Occurrence - % in 80 Samples(6)	Occurrence - % in 50 Samples(7)
Themeda triandra	33	29	43
Pennisetum mezianum	14	19	3
Cynodon dactylon	8	13	5
Microchloa kunthii	7	7	12
Aristida adscensionis	-)	-)	6
Aristida adoensis	-) 6	-) 6	3
Aristida keniensis	-)	-)	2
Eustachys paspaloides	4	3	2
Harpachne schimperi	3	3	6
Sporobolus spp.	3	3	tr
Eragrostis braunii	-)	-)	3
Eragrostis spp.	-) 3	-) 3	tr
Andropogon greenwayii	2	1	4
Bothriochloa insculpta	2	4	tr
Panicum spp.	2	tr	tr
Chloris pycnothrix	2	tr	tr

[continued on next page]

Table 16. Continued.

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Pennisetum stramineum	1	2	1
Chloris spp.	1	tr	tr
Hyparrhenia lintonii	tr	tr	1
Trace grasses (see Table 17)	1	2	4
Herbs (c.f. Table 17)	3	2	tr
Seeds	tr	tr	-

---

1. Rumen and Reticulum.

2. All figures rounded to nearest per cent, and figures less than one per cent are listed as trace (tr.). Items appearing as traces in all three methods of analysis are listed in Table 17.

3. Nomenclature follows Bogdan (1958) and East African Herbarium.

4. Identified in the field by the L.M. Talbots.

5. Identified at the Fauna Research Unit Laboratory, Kenya Game Department, Nairobi, by the D.R.M. Stewarts.

6. Representing 80 animals. Average of about 30 items per sample; about 25 per cent unidentified.

7. Representing 73 animals. Average of about 50 items identified at random per sample; about five per cent unidentified.

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Table 17. Trace Items(1) in Stomach(2) Contents of Western White-Bearded Wildebeests.

Grasses:

Cenchrus ciliaris
Chloris gayana
Chloris myriostachya
Chrysochloa orientalis
Chrysopogon aucheri
var. *quinqueplumis*
Cymbopogon excavatus
Cynodon plectostachyus
Eragrostis cilianensis
Eragrostis exasperata
Eragrostis tenuifolia
Heteropogon contortus
Hyparrhenia spp.

Panicum maximum
Panicum spp.
Sporobolus discosporus
Sporobolus filipes
Sporobolus fimbriatus
var. *latifolius*
Sporobolus marginatus
Sporobolus phyllotrichus
Sporobolus pilliferus
Sporobolus pyramidalis
Sporobolus spicatus
Sporobolus stapfianus

Others:

Sida spp.
Justicia spp.
Cyperus sp.
Trifolium sp.
Wildebeest tail and mane hair.

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(1) Items representing less than one per cent of stomach contents by all three methods of analysis (c.f. Table 16).

(2) Rumen and reticulum.

*136 would counts of items in relatively small samples from
*125 the stomachs. However, the rangeland of the study area, which is the source of the food items, contains such a wealth of grasses and grassland plants that we considered it very important to get some control or verification of the estimates.

This check is provided by the item counts (Columns 2 and 3 in Table 16). The microscopic occurrence count (Column 3) representing 50 items per sample, with only about five per cent of these unidentified, should give a more accurate picture than the macroscopic counts (Column 2) which represent about 30 items per sample, about 25 per cent of which were unidentified.

The three columns show a similar ranking and relationship between the different food items. The one significant exception is *Pennisetum mezianum* which ranks second in the macroscopic identifications but about 8th in the microscopic results. Stewart (Pers. comm. dated 31 July, 1962) wrote that "We feel we may be slightly 'low' on *Pennisetum mezianum*, which often has a thin cuticle with inconspicuous characters making certain identification difficult. No such factor affects the other species..." In view of Stewart's note, and the fact

*136 *125 that *Pennisetum mezianum* is relatively easy to identify macroscopically when it is fresh in the field, we consider there is no question that it ranks high in importance.

A given number of relatively small-leaved grasses would have less volume than the same number of grasses with larger leaves. This factor is apparently reflected in the differences between Columns 1 and 3 in Table 16, where the relatively small-leaved grasses such as *Microchloa kunthii*, *Aristida adscensionis*, and *Harpachne schimperi* show higher item counts than volume estimates; while the relatively large-leaved grasses such as *Cynodon dactylon* indicate the reverse.

Another factor affecting direct comparison of the three columns is the size of the sample. The volume estimates are taken from about twice as many animals and three times as many samples as the microscopic occurrence figures.

*125 Therefore we consider that there is very satisfactory agreement between the results of the different analyses. The exhaustive microscopic analyses of the Stewarts appear to confirm in general pattern, and largely in detail, the estimates of volume made in the

#136 field. Their work also produced a number of trace
#125 items that were not noted in the field analysis,. Most of the trace grasses on Table 17 were identified by the Stewarts.

The results in Table 16 are expressed in percentages to facilitate comparison. However, estimations of volume are necessarily approximate, and the occurrence figures are taken from relatively small samples. Therefore it should be stressed that the figures given do not necessarily reflect the exact mathematical fractions of each species eaten by the wildebeests. The figures do indicate the rank of importance of each food species in the diet of the wildebeests. In terms of composition by volume, the first column (Table 16) probably reflects -- as closely as possible with present knowledge -- the average yearlong diet of the wildebeests in the study area during the period of study. One would not expect to find just this composition in the stomach of any individual animal. The plants involved do not all grow in the same area at the same time, and normally only about eight different food items are found in the contents of a wildebeest stomach. Also, some of the trace items come from wildebeest calves which apparently experiment with different foods before they adopt the adult diet.

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From Table 16 one can make the following generalizations: Wildebeests are grazing animals and their diet is almost exclusively grass. _Themeda triandra_ is by far the most important single food species. Five grasses appear to make up between two thirds and three fourths of the yearlong diet, and ten grasses make up about 90 per cent. Therefore the wildebeests appear to be remarkably specific and consistent in their yearlong, range-wide diet.

The same characteristic holds true for other ungulates within the study area (Talbot, 1962). In fact, one of the most significant results of our ecological study has been the documentation of the complementary and non-duplicating preferred diets of the various species of plains herbivores.

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Whenever it is available the wildebeests eat very short green grass. They prefer grass just sprouting, and once it has reached about 4 inches they usually pass on. Where no other grass is available, wildebeests will remain on an area and keep it grazed short, but they will rarely eat leaves or stalks much longer than four inches.

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During their seasonal movements throughout their range, they follow, as much as possible, available sprouting short green grass. Except for entirely rainless periods, the wildebeests spend the year on this type of food. Grass will sprout usually within 24 to 36 hours after a rain. The wildebeest population is constantly on the move apparently following these rains to obtain the sprouting grass. Their diet, therefore, is remarkably uniform throughout the year.

The weight of stomach (rumen and reticulum) fill averages 13.1 per cent(± 0.9 per cent) of total body weight for all classes of wildebeests. Stomach (rumen and reticulum) fill averages about 60 pounds for adult males, 50 pounds for adult females, and 21 pounds for males and females under 12 months old. Stomach fill data are presented in Table 18.

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To get an approximation of the relative weights of important food items we multiplied the total wet weight of the rumen and reticulum contents by the percentage of significant items in Column 1 of Table 16, using the method described by Buss (1961:134). The result for an average adult male is given in Table 19. It is emphasized however that these results present a generalized yearlong average for animals from the whole

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Table 18. Stomach[1] Fill Data on White-Bearded Wildebeests in Western Masailand.

Age Class	Sex	Number in Sample	Minimum Weight, Pounds	Maximum Weight, Pounds	Average Weight, Pounds	Per Cent - Ave. Stomach Fill of Ave. Body Weight
Adult	Male	19	34	82	60.7	13.59
Adult	Female	32	26	77	50.5	14.06
Young[2]	Male	20	1	58	21.5	12.22
Young[2]	Female	21	15	33	21	12.43

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(1) Rumen and reticulum only.

(2) Animals under 12 months of age.

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Table 19. *Generalized Yearlong Average Stomach*(1) *Contents*(2) *of an Adult Male Western White-Bearded Wildebeest*.

Species	Total Pounds Consumed
Themeda triandra	20.0
Pennisetum spp. (mostly *P. mezianum*)	9.1
Cynodon spp. (mostly *C. dactylon*)	4.9
Microchloa kunthii	4.3
Aristida spp.	3.6
Digitaria spp.	3.0
Eragrostis spp.	2.4
Eustachys paspaloides	2.4
Harpachne schimperi	2.4
Sporobolis spp.	1.8
Andropogon greenwayii	1.8
Other grass species	4.2 + traces
Non-grass forage (seeds, herbs, etc.)	0.6 + traces
Total	60.5 + traces

---

(1) Rumen and reticulum.

(2) This is a yearlong average for animals from the whole study area, based on Column I of Table 16. It does not describe the stomach contents of any given wildebeest, but provides a rough index of the relative amounts of important food items eaten by the wildebeests.

(3) Wet weight, method used by Buss (1961).

*136 *125 area, based on estimates of the volume of items in the stomach contents. They do not describe the stomach contents of any given wildebeest, but rather they provide a rough index of the relative amounts of important food items eaten by the wildebeests.

*136 Table 16 shows that by far the most important single grass species in the diet of the wildebeests is red oats grass (Themeda triandra). Grzimek and Grzimek (1960a:42 et.seq.), on the other hand, stated that Themeda triandra was refused by the wild animals. They apparently based their statement on observing what grasses were still standing after the wild animals had grazed through an area, and on which grasses appeared to be grazed. Wildebeests almost exclusively graze low grass, leaving the stems and taller leaves standing. A stand of red oats grass can be very heavily grazed by wildebeests and enough stalks and leaves will still be standing to create the impression that the species is uneaten. As noted above and detailed in (Talbot (1962:131-132) under the plainsland conditions of the study area the only way to determine what foods different ungulates eat is to examine what is actually inside the animals or to analyse their faeces.

*233
*136
231

Of the ten species of grass which make up 90 per cent of the wildebeests' diet as calculated in Table 16, only two, _Themeda triandra_ and _Cynodon dactylon_ are also important forage for domestic livestock. _Themeda triandra_ is excellent forage while _Cynodon dactylon_ varies widely in its palatability for livestock (Bogdan, 1958; Heady, 1960). _Themeda triandra_ rapidly disappears from overgrazed ranges. _Cynodon dactylon_, however, thrives on disturbed ground and is more tolerant of heavy grazing than _Themeda_. The other grasses which are important in the wildebeests' diet are rarely eaten by domestic livestock. On overgrazed ranges in the study area they become dominant after the grasses such as _Themeda_ which are more palatable to livestock are grazed out (Heady, 1960; Talbot, 1960c). In general, these other grasses "are low producing plants of poor palatability [for domestic livestock, L.T.] and their dominance indicates poor condition ranges." (Heady, 1960:13).

Therefore there is direct competition between wildebeests and domestic livestock for only two species of grasses; one of these, however, is the most important single item in the wildebeests' diet. It also is one of the first grasses to disappear under heavy

*233
*136 231 livestock grazing. Consequently, overgrazing by domestic/ livestock can seriously reduce the carrying capacity of rangeland for wildebeests, even though there is relatively little direct competition between them in terms of total numbers of grass species involved.

*136 *125 (b) Other Ungulates: In addition to the wildebeest data, we have stomach sample analyses from 130 other animals of ten species: Thomson's gazelle, Grant's gazelle, topi, kongoni, impala, zebra, buffalo, dik dik, giraffe, and rhinoceros. We also have observational data from elephants, giraffes and rhinos whose food habits, unlike the plainsland graziers, are possible to identify from observation alone.

*136 The results of these studies show that each ungulate species has a preferred diet which is to a large degree complementary to -- not duplicating -- the diets of the other ungulates. These diets are maintained throughout the year, where necessary the animals traveling long distances to find their preferred foods at the preferred stage of growth. The diets involve different classes of food (e.g. trees, shrubs, forbs, grasses), different species of food plant within a class, and different stages of growth of the same food plant.

*136

Tables 20 through 24 were compiled in 1960 (Talbot, 1962). Although they refer to relatively few animals, they illustrate some of the specific preferences of the various ungulates involved. Subsequent collections have shown even more clearly the complementary nature of the ungulates' diets, either as to species chosen or to the stage of growth of a given species.

Red oats grass (Themeda triandra) is a good example. It is the most important single item in the diets of wildebeests, zebras, and topis. By estimated volume it accounts for about 33 per cent of the wildebeests stomach fill and 22 per cent of both zebra and topi. As noted above the wildebeests eat this grass when it is green and sprouting, normally under about four inches. Zebra eat more mature green leaves and stalks. Topis, on the other hand, eat it mostly when it is mature to dry.

Research undertaken in cooperation with the Animal Husbandry Division of E.A.A.F.R.O. (Payne, 1961), while not completed, indicates that there are differences between the various ungulate species in physiology, especially of the digestive tract. These differences appear to be correlated with the diets of the animals,

[TEXT CONTINUED ON PAGE 259]

*136

Table 20.

Preliminary Stomach Sample Analyses based on Item Counts.

Wildebeests.

Animal species: White-bearded Wildebeest (*Gorgon taurinus*).
Number of stomachs examined: 60 (males, females, and young).
Location: Kenya, Narok District: Loita Plains and Mara region 44
Kenya, Kajiado District: Athi Plains and Rift Valley 4
Tanganyika, Serengeti Plains south of park boundary 10
Date of collection: September, 1959—December, 1960.

1. Class of Foods:
Grass: 98% (80% identified, 20% unidentified)
Other: 2% (trace of *Sida schimperi*, *Justicia* sp., seeds, the rest unidentified).

2. Total Dry Material:

% of stomachs contained	*% dry material*
72·4	0–10
8·6	11–33
10·3	34–67
8·6	68–100

3. Food Analysis:

*[137]

I Item	II % in total sample stomach contents	III Portion of plant eaten: % within species Green leaves	IV Green stalks	V Stalks and leaves, dry	VI Seed heads	VII Runners roots
Grass:						
Thomoda triandra	26	78	14	6	2	—
Pennisetum mezianum	19	52	33	15	2	—
Cynodon dactylon	12	63	28	7	—	2
Aristida spp.	5	64	26	5	—	5
Bothriochloa insculpta	4	74	26	—	—	—
Eragrostis spp.	3	65	26	9	—	—
Microchloa kunthii	3	62	24	—	14	—
Digitaria spp.	3	90	10	—	—	—
Sporobolis spp.	3	63	21	16	—	—
Chloris sp.	trace	75	25	—	—	—
Hyparrhenia sp.	trace	75	25	—	—	—
Panicum sp.	trace	67	33	—	—	—
Hyparrhenia lintonii	trace	50	50	—	—	—
Grass—unidentified	20					
Other:						
Herbs—unidentified	2	100	—	—	—	—
Seeds—unidentified	trace	—	—	—	100	—
Sida schimperiana	trace	100	—	—	—	—
Justica sp.	trace	100	—	—	—	—

REMARKS.—There was no significant difference between stomach contents of the wildebeest from the three locations. Calves contained some grass in the rumen from the age of about ten days. There does not appear to be any significant difference between grasses eaten by the young and those eaten by adults. Milk was found in the abomasum in some young animals up to the age of 16 months, although most are completely weaned by 12 months.

Table 21.

*136 Preliminary Stomach Sample Analyses based on Item Counts.

Topis.

Animal species: Topi (*Damaliscus korrigum*).

Number of stomachs examined: 5 (male and female).

Location: Kenya, Narok District; Mara region.

Date of collection: July, 1960—December, 1960.

1. **Class of Foods:**
    - Grass: 97% (65% identified, 35% unidentified).
    - Other: 3% (all an unidentified species of *Cyperaceae*).
2. **Total Dry Material:** *% of stomachs* contained 100 *% dry material* 67–100

*[137] 3. **Food Analysis:**

I Item	II % in total sample stomach contents	III	IV	V	VI	VII
		Portion of plant eaten: % within species				
		Green leaves	Green stalks	Stalks and leaves, dry	Seed heads	Runners roots
Grass:						
Cynodon dactylon	14	21	5	74	—	—
Aristida spp.	13	18	41	41	—	—
Pennisetum mezianum	9	trace	17	83	—	—
Themeda triandra	8	55	—	45	—	—
Harpachne schimperi	8	27	27	46	—	—
Eragrostis sp.	7	—	33	67	—	—
Bothriochloa insculpta	4	20	—	80	—	—
Unidentified	34					
Other:						
Cyperaceae (Carex ?)	3	100	—	—	—	—

REMARKS.—Green material of all species taken was present at the sites where each of the animals involved was collected, and the stomach contents of wildebeest collected at the same time on the same location contained about 100% green material. Therefore the preponderance of dry material in the topi stomachs reflects choice rather than necessity.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

Table 22.

*136 Preliminary Stomach Sample Analyses based on Item Counts.

Thomson's Gazelles.

Animal Species: Thomson's Gazelle (*Gazella thomsonii*).

Number of stomachs examined: 10 (males, females, and young).

Location: Kenya, Narok District: Loita Plains and Mara region 7
Tanganyika, Serengeti Plains south of park boundary 3

Date of collection: February, 1960—December, 1960.

1. **Class of Foods:**
   - Grass: 80% (82% identified, 18% unidentified).
   - Other: 20% (69% identified, 31% unidentified).

2. **Total Dry Material:**

% *of stomachs* contained	% *dry material*
50	0-10
50	11-67

3. **Food Analysis:**

*(137]

I Item	II % in total sample stomach contents	III Portion of plant eaten: % within species Green leaves	IV Green stalks	V Stalks and leaves, dry	VI Seed heads	VII Runners roots
Grass:						
Cynodon dactylon	21	57	43	—	—	—
Pennisetum mezianum	15	80	20	—	—	—
Panicum sp.	12	50	50	—	—	—
Digitaria spp.	7	40	60	—	—	—
Eragrostis spp.	7	40	60	—	—	—
Themeda triandra	3	100	—	—	—	—
Unidentified	15					
Other:						
Sida schimperiana	5	100	—	—	—	—
Solanum sp.	4	70	—	—	30	—
Justicia sp.	2	100	—	—	—	—
Leguminous seeds	2	—	—	—	100	—
Courbonia sp.	1	70	—	—	30	—
Unidentified	6					

19: Talbot E-4,5 (1956-1962)1964 FL12 Masai FL12

Table 23.

*136 Preliminary Stomach Sample Analyses based on Item Counts.

Grant's Gazelles.

Animal species: Grant's Gazelle (*Gazella granti*).

Number of stomachs examined: 10 (males, females, and young).

Location: Tanganyika, Serengeti Plains south of park boundary 8
Kenya, Narok District, Mara region 2

Date of collection: February, 1960—December, 1960.

1. Class of Foods:
    Grass: 40% (84% identified, 16% unidentified).
    Other: 60% (67% identified, 33% unidentified).

2. Total Dry Material:

% of stomachs contained	*% dry material*
30	0–33
40	34–67
30	68–100

3. Food Analysis:

*[137]

I Item	II % in total sample stomach contents	III	IV	V	VI	VII
		Portion of plant eaten: % within species				
		Green leaves	Green stalks	Stalks and leaves, dry	Seed heads	Runners roots
Grass:						
Harpachne schimperi	10	67	33	—	—	—
Cynodon dactylon	9	80	20	—	—	—
Hyparrhenia lintonii	9	80	20	—	—	—
Microchloa kunthii	6	50	30	—	20	—
Themeda triandra	trace	80	20	—	—	—
Unidentified	6	5	70	25	—	—
Other:						
Indigofera sp.	11	60	40	—	—	—
Sida schimperiana	11	90	10	—	—	—
Solanum sp.	6	80	—	—	20	—
Legume seeds, pods	4	—	—	—	100	—
Astor sp.	4	60	40	—	—	—
Balanities aegyptica	2	100	—	—	—	—
Unidentified	22					

REMARKS.—Of the animals considered in this paper the Grant's gazelle has the highest per cent consumption of items other than grass. In spite of the availability of other food species, the principal species of grass and other foods chosen by the Grant's gazelle are those which invade or become dominant in overgrazed, abused, grasslands in the study area (Heady, 1959; Talbot, 1960). With the exception of *Cynodon dactylon*, this animal's food preferences are complementary to those of domestic livestock and the other wild animals studied.

Table 24.

*136 Preliminary Stomach Sample Analyses based on Item Counts.

Impala.

Animal species: Impala (*Aepyceros melampus*).

Number of stomachs: 7 (male, female, and young).

Location: Kenya, Narok District, Mara region	6
Kenya, Kajiado District, Rift Valley	1

Date of collection: January, 1960—December, 1960.

1. Class of Foods:
   Grass: 56% (74% identified, 26% unidentified).
   Other: 44% (67% identified, 33% unidentified).

2. Total Dry Material: *% of stomachs* contained *% dry material*
   100 0–33

3. Food Analysis:

*[137]

I Item	II % in total sample stomach contents	III	IV	V	VI	VII
		Portion of plant eaten: % within species				
		Green leaves	Green stalks	Stalks and leaves, dry	Seed heads	Runners roots
Grass:						
Themeda triandra	11	67	33	—	—	—
Pennisetum mezianum	10	31	31	38	—	—
Panicum maximum	10	77	23	—	—	—
Chloris gayana	7	56	44	—	—	—
Cynodon dactylon	4	83	—	17	—	—
Unidentified	15					
Other:						
Solanum sp.	15	60	—	—	40	—
Legume seeds, pods	15	—	—	—	100	—
Euclea schimperi	4	100	—	—	—	—
Unidentified	15	100	—	—	—	—

*136 particularly the protein and fiber content of their preferred diets and their water requirements (Ledger, et. al., 1961). It appears, then, that the complementary diets of these animals represent not only foods that are preferred, but also foods that provide the optimum nutrition for which the digestive tracts of the animals are adapted.

Comparison between Eastern and Western Masailand illustrates this point. In Western Masailand the ungulates are free to move throughout the area, following their preferred food plants at the preferred stages of growth. In Eastern Masailand, as described above, the ungulates are restricted in movement and their ranges and water supplies are depleted.

Several lines of evidence -- including age of females at their first breeding, timing and success of breeding, pre- and post-natal survival and differential sexual mortality of young, resistence of population to drought stress, and biomass, indicate that the animals in Eastern Masailand are maintained on a low plane of nutrition. Wildebeest serve as an example.

Under optimum conditions in the study area

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

*136 83 per cent of the yearling wildebeest cows and 95 per cent of the adult cows are bred annually; in Eastern Masailand yearlings apparently rarely breed, only about one third of the two year old cows and about 80 per cent of the older cows are bred. Pre- and post-natal calf survival is far higher in the study area where the calf: cow ratio at six months of age is 49:100, than in Eastern Masailand where it is 18:100 (Lamprey, pers Comm.). Survival of male calves may be another indication of the level of nutrition of the population (Robinette, et. al., 1957). In the study area adult bulls outnumber cows (108:100), while in Eastern Masailand the reverse is the case (49:100) (Lamprey, op.cit.). During drought years in the study area the wildebeests moved away from the driest conditions, and no change was noted in reproductive success. In Eastern Masailand, in the Athi-Kapiti Plains for example, the wildebeests were unable to move away from drought conditions and the population suffered accordingly. In the severe drought of 1961, no wildebeest calves survived, possibly a third of the adult population died, breeding was delayed about three months, and almost no calves were produced during the calving season of 1962. Prior to the drought, in the Athi-Kapiti Plains the biomass of three key species, wildebeest, zebra, and kongoni, was about 7,520 pounds per square mile; this biomass had dropped to 3,525 pounds per square mile after

*136 the drought, due to death and possibly some emigration (Kenya Game Dept., 1962). During the same period, the biomass of these three species in the study area remained at about 16,890 pounds per square mile.

Conclusions: The result of these non-duplicating food preferences is that virtually all of the available vegetation can be used efficiently to support the biomass of mixed wild ungulates. Whereas, when cattle, goats, and sheep graze, only one class of food -- grass -- and only a few species within that class are the preferred forage and most efficient source of nutrition (Heady, 1960).

The wild ungulates of Western Masailand can be divided generally into three groups on the basis of their food requirements: the grazing animals, browsing animals, and the mixed feeders. The mixed feeders such as impala and dik dik feed on both grass and browse. They are able to find their optimum nutrition throughout the year in a relatively limited area, alternating between eating grasses and browse much as some of our deer (Taber and Dasmann, 1958). The grazing animals must constantly move from one place to another to find their grasses and forbs at the preferred stage of growth, and to follow their water requirements.

136 Of necessity then, most grazing animals are migratory. Zebras and wildebeests are the obvious examples. But even elephants and buffaloes make often-irregular but sometimes extensive movements within the bush habitat, apparently correlated with the availability of the coarse forest grasses which make up the bulk of their food, and with water. Only two of the ungulate species considered above are nearly pure browsers, giraffe and rhino. Rhino are resident near water, while giraffe may make short seasonal migrations.

Water Requirements

The water requirements of the grassland ungulates range from wildebeests and buffaloes which rarely go without water for more than two or three days to Grant's gazelle and oryx which may spend much of the dry season in areas completely devoid of surface water. Thomson's gazelles are somewhat intermediate. Brooks (1961) notes that they prefer to drink at daily intervals, but they will remain in an area longer than wildebeests and zebras after surface water has dried up, and a few old males may spend much of the dry season on open plains.

Some arid land animals may have a water-saving mechanism to enable them to survive particularly serious

#136 drought periods. Work now in progress at the East African Agriculture and Forestry Research Organization, Muguga, Kenya, is showing that in dry periods when protein level in the dried grass is low, nitrogen in the food may be recycled in the body rather than being excreted in urea (Livingston, 1961; Livingston, et. al., 1962). In addition to saving nitrogen and enabling the animal to subsist on food with far lower available protein content, this adaptation would save water, as water would not be required for urine excretion. This mechanism may operate in wildebeests under extreme drought conditions.
#125
#126
#136 The immobilizing drug Flaxedil (Gallamine Triethiodide) is excreted through the kidneys at a standard rate under normal conditions (Talbot and Talbot, 1962:82). In the case of seven animals immobilized at the height of a drought the drug was not excreted for periods of up to eight hours or longer beyond the normal period, which would indicate that the rate of excretion of waste from the blood had been greatly reduced -- a direct result of the nitrogen and water saving mechanism described by Livingston et. al.

#736

Migrations

The most striking single aspect of the East African plains wildlife is the periodical concentration and mass movement of the antelopes and zebras. In 1929

*136 Johnson (p.270) wrote, "Many sights we have seen in Africa still impress us as being unique; but for drama, for power, for sustained excitement, no other experience that we have ever had approached those hectic days that we spent on the finges and in the heart of the ... zebras and wildebeeste that made up the great migration of 1928."

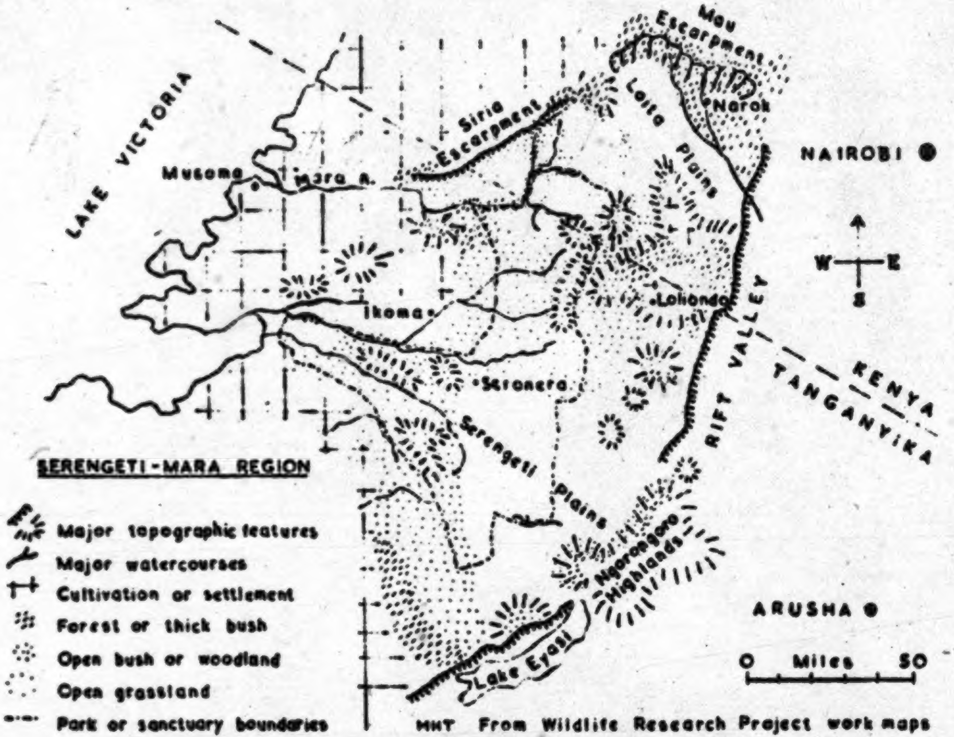
In terms of total numbers of animals, the Serengeti-Mara migrations involve roughly one million animals. These numbers seem rather insignificant when compared to the many millions of animals estimated in the migrations of American bison and barren ground caribou (Banfield, 1954; Garretson, 1938; Seton, 1927). However, in terms of population density the Serengeti-Mara region probably supports a higher population than did the American areas. The densities quoted by Petrides (1956:533) for bison, or mixed populations of bison, elk, deer, and cattle on the American plains ranged from 6 to 35 animals per square mile. The Serengeti-Mara region appears to support a mixed population of ungulates (including Thomsons and Grant's gazelles, wildebeests, zebras, topis, kongonis, and elands, but not including the native livestock) of very roughly 100 animals per square mile.

Except for the resident mixed feeders such as the

*136 impala, dik dik, and reed buck, virtually all ungulates in Western Masailand are somewhat migratory. In some cases the migrations involve movements between different levels on the larger hills or mountains. Most migrations involve lateral movements from dry season to wet season habitats that are determined by availability of particular kinds of food and of water.

The movements of each species of ungulate are correlated with that species' particular nutritional requirements. Therefore not all animals follow the same movement patterns at the same times. This point is illustrated by comparing the distribution maps of several of the species counted during the May, 1961 aerial census (Fig. 41 - 45).

Wildebeests seek open areas and relatively flat terrain. Zebras will move through thick bush and over rough terrain. We have found them grazing on the tops of the steep, brushy quartzite hills north of the Serengeti Plain, while wildebeests generally avoid even the flanks of the hills. Topis and kongonis are found scattered widely through bush and open woodland on a variety of types of terrain. Buffaloes frequent thickly wooded areas on hillsides or along watercourses, but where not hunted they will graze some in open plains. Elephants are almost exclusively bush or forest animals.


LAKE VICTORIA
Musoma
Mara R.
Siria Escarpment
Mau Escarpment
Loita Plains
Narok
NAIROBI
Ikoma
Lolionda
Seronera
Serengeti Plains
RIFT VALLEY
KENYA
TANGANYIKA
Ngorongoro Highlands
Lake Eyasi
ARUSHA
W E S
0 Miles 50
SERENGETI-MARA REGION
Major topographic features
Major watercourses
Cultivation or settlement
Forest or thick bush
Open bush or woodland
Open grassland
Park or sanctuary boundaries

MHT From Wildlife Research Project work maps

Figure 41. Reference Map of the Study Area for use with Distribution Maps, Figures 42, 43, 44, and 45.

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133

102
†136

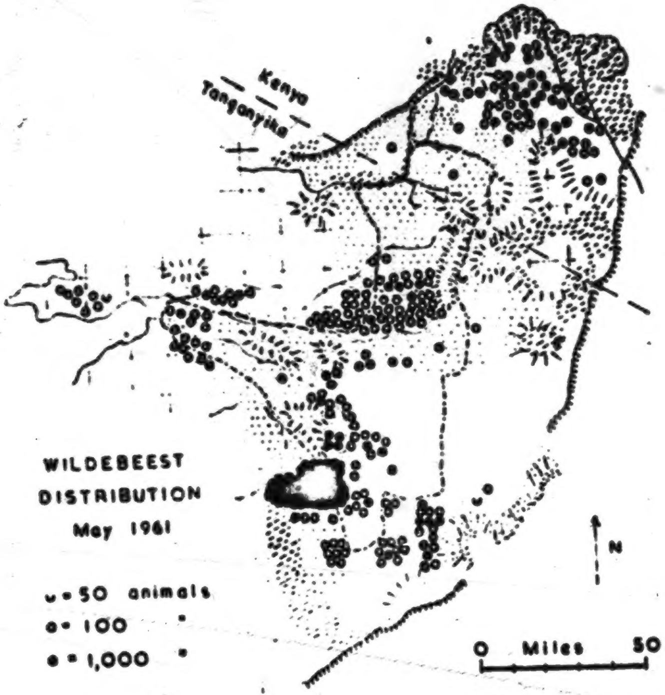
Kenya
Tanganyika
WILDEBEEST
DISTRIBUTION
May 1961
◡ = 50 animals
○ = 100
● = 1,000
N
0 Miles 50

Figure 42.

102
*136

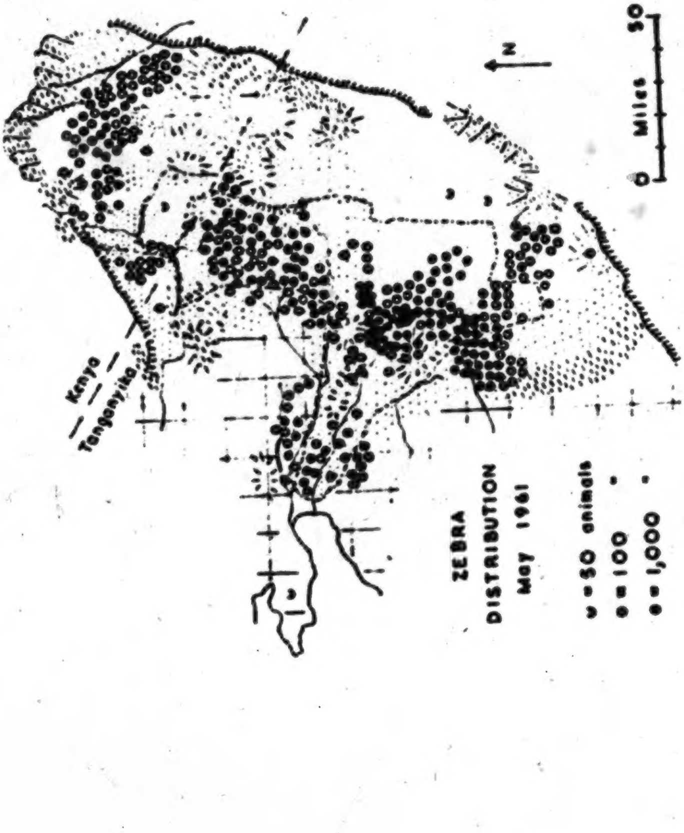
Kenya
Tanganyika
N
0 Miles 50
ZEBRA
DISTRIBUTION
May 1961
◡ = 50 animals
○ = 100 "
● = 1,000 "

Figure 43.

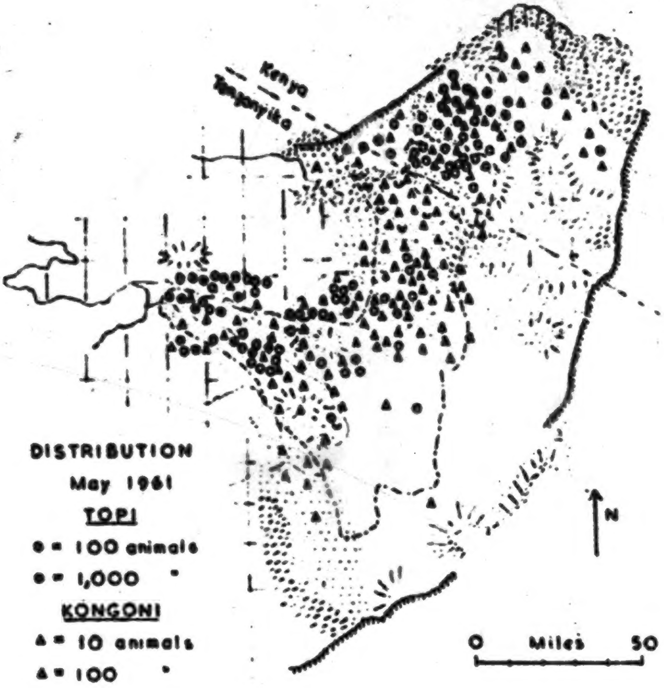
Kenya
Tanganyika
DISTRIBUTION
May 1961
TOPI
● = 100 animals
● = 1,000 "
KONGONI
▲ = 10 animals
▲ = 100 "
N
0 Miles 50

Figure 44.

102
*136

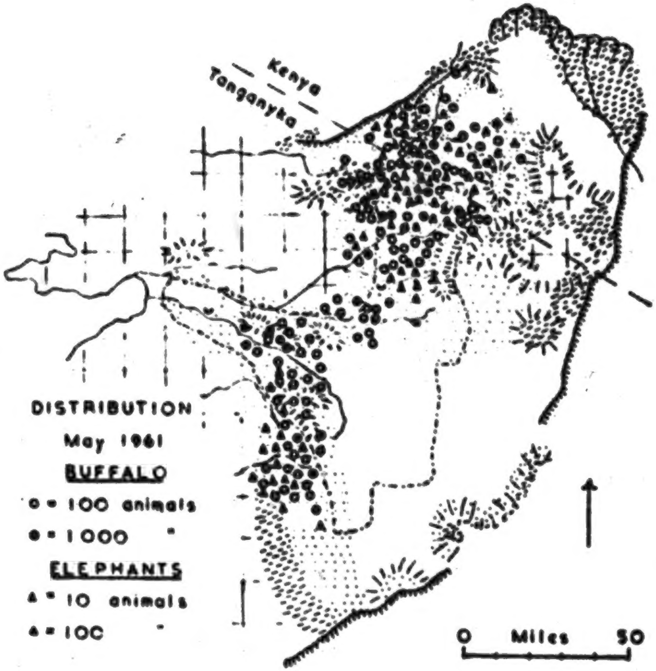
Kenya
Tanganyika
DISTRIBUTION
May 1961
BUFFALO
○ = 100 animals
● = 1000 "
ELEPHANTS
△ = 10 animals
▲ = 100 "
0 Miles 50

Figure 45.

*136 Some migrations involve quite short distances while others cover hundreds of miles. Most movements of the buffaloes appear limited under twenty miles; Thomson's gazelles 30 to 50 miles, and elands considerably farther. One marked topi traveled a distance of something over 120 miles. Wildebeests may travel over 1,000 miles during a year's migrations.

121
*136
128 Migrations are an essential factor in maintenance of the grassland ecosystem. The basic factors involved in migration include specific food and water requirements, environmental factors that affect their availability, environmental stimuli and the animals' response to them. In specific detail, of course, these factors vary from species to species, but the basic factors are common to all. Consequently, more can be learned of the phenomenon of migration from an examination in depth of one species than from superficial accounts of the migrations of each species. As described above, the wildebeests appear to be the key ungulate species in Western Masailand, so in the following description of migration the wildebeests are used as the example.

121
*136

True migration was defined by Bourlière (1955:203) as "seasonal and regular passages between an area where reproduction takes place and a zone in which the winter is spent... " As he points out subsequently, however, migration is not well known in mammals and the examples studied do not necessarily fit the above definition. In wildebeest migration, passage is neither seasonal nor regular, and reproduction takes place and winter is spent often during the migratory movements. The movements of the wildebeests do not fit the definition of true migration. However

121 *136 similarly erratic movements in caribou, bison, and other animals have been described as "migratory behavior" (Bourlière, 1955; Matthews, 1955; Seton, 1927). "Migration" is the term in common use to describe wildebeest movements so I shall continue to use it as such, while emphasizing the distinction between the movements of wildebeests and those of true migratory species.

128 *136 A distinction might be drawn between the large scale migrations of wildebeests, which may cover several hundred miles in a few days, weeks, or months; and local, small scale movements. As will be shown below, the only apparent difference between these types of movement is a matter of distance. The factors involved appear identical, so the two will be considered together.

*136 Previous Knowledge and Beliefs about Wildebeest Migrations: It was recognized early that the wildebeests in Western Masailand migrated long distances. In 1912 (Kenya Game Dept., 1912) the Chief Game Warden of Kenya noted: " I am inclined to think they [the wildebeest] must go into German Territory and down to the far end of the Southern Reserve...." He based this observation on the fluctuations in numbers of wildebeests in the Mara area. He apparently assumed that the wildebeests traveled in a south-easterly direction, into and through the Rift Valley.

*136 Some may have done this, but in view of present knowledge, it would appear that most of the animals involved moved south-southwest toward the Serengeti Plain.

In 1920 a Game Warden was appointed to Narok District (Kenya Game Dept., 1920), and his area of responsibility included the Kenya portion of the Serengeti-Mara region. In 1921 he noted (Kenya Game Dept., 1921), "During the very dry weather a large proportion of wildebeest migrate to the Serengeti Plains in Tanganyika Territory but immediately the grass becomes green again in my district they can be seen in their thousands."

In the Kenya Game Department report of 1927, the Chief Game Warden noted the complaints of the Masai that wildebeest were competing with their cattle herds, but said that it would not do much good to shoot the wildebeests because of the "apparently inexhaustable wildebeest reservoir" over the border in Tanganyika.

A then-current belief involved a supposed migratory movement of wildebeest between the Athi Plains in Kenya southwest through the Rift to the Serengeti Plains (Johnson, 1929:266). This movement appears most unlikely because of the intervening west wall of the Rift, which at

*136 the point of crossing (for animals trying to reach the Serengeti) is almost vertical and over 2,000 feet high.

More recently the migration routes were described from the then-available data by Brooks (1961), Grzimek and Grzimek (1960a), Pearsall (1957), and Swynnerton (1958) for Tanganyika, and by Darling (1960) for Kenya. In general they agreed that the wildebeests moved to the open grass plains areas when it rained and the grass there was green, and that they moved off when the plains dried; all noted that at least some of the animals moved to or toward the Bologonja area (near the Kenya-Tanganyika border) but they did not believe that any significant inter-territorial exchange of animals took place.

The major point of disagreement between the observers in Tanganyika involved the role of Ngorongoro Crater in the Serengeti migrations. Pearsall (op. cit.) and Swynnerton (op. cit.) both described a seasonal movement of wildebeests between the Crater and the eastern Serengeti Plain. Grzimek and Grzimek (1960a:14) state that "As we discovered later, this seems to be an erroneous conclusion." On the basis of their aerial count in the Crater on 3rd January, 1958, aerial reconnaissances during their five months' survey that year, and an estimate of the Crater animals by park personnel made on 6th March, 1959, *136 Grzimek and Grzimek concluded that there was no significant movement of wildebeests or other animals between the Crater and the lower plains, and that the wildebeests observed on the eastern Serengeti Plain near the foot of the Ngorongoro Highlands had come from the west or north.

Detailed descriptions of the monthly movements of the wildebeests in Tanganyika have been presented in the monthly reports of the Serengeti National Park (1957-1963), some of which were also used by Grzimek and Grzimek (1960a:29 et. seq.). Relatively fixed regular migration routes and seasonal movments were described and mapped by Grzimek and Grzimek. However, Brooks (op. cit.), Darling (op. cit.), Pearsall (op. cit.) and Swynnerton (op. cit.) all noted that the movements of all the plains animals were strongly affected by the irregular rainfall patterns and therefore were relatively flexible.

The obvious relationship between the wildebeests' movements, rainfall and grass was noted by many other observers (Kenya Game Dept., 1910, 1911, 1912; Moore, 1960; Percival, 1928; Willis, 1930). Swynnerton (op. cit.) also postulated avoidance of long grass and bush, flooding, and scarcity of feed or fouling of feed and water, and instinct to calve in traditional areas as factors affecting migrations. Other factors mentioned in the literature include poaching

*136(Moore, op. cit.) and predation (Percival, op. cit.).

Results of the Present Study: Since detailed descriptions of monthly movements of the wildebeests are available elsewhere, and in any case, no two seasons' movements are the same, I shall not include such a description here. Instead, I shall summarize briefly our observation on general patterns, distances, and the causal factors involved.

(a) *General Pattern:* During the wet seasons the wildebeests congregate on the open grass plains of the Serengeti and the Loita, where they remain so long as green grass and water remain. As noted above during this time the animals are constantly moving, grouping into large herds, dispersing, then regrouping. As surface water and grazing begin to dry the animals leave the plains. During the dry periods they disperse through the surrounding bush country, eddying and flowing throughout a vast area of bush or acacia woodland apparently seeking water supplies and patches of green grass brought on by local showers.

In Tanganyika the general dry season movements are west and north from the central plains, then north and east toward or into Kenya, then south or southwest back to

*136 the Serengeti Plain. In Kenya, the movements are southwest from the Loita Plain to and beyond the Tanganyika border or the Mara River, then north and east back to the Loita Plain. Thus the migration paths of the wildebeests in the study area are very roughly circular, as are those of bison and caribou (Matthews, 1955), and are generally clockwise in direction.

There is significant mingling and interchange of population between the northern and southern migration "circles." The movements are highly irregular and involve constant shifts of direction, doubling and circling back depending on the factors described below. The route described is a generalized average and some years certain areas may be visited several times or be missed altogether. No two years' or seasons' movements necessarily will be alike.

(b) Distance Traveled. The southern "circle" has a maximum east-west spread of about 120 miles airline, and north-south spread of about 140 miles. The point to point distance clocked on our Land-Rover odometer as we followed the main concentrations around the southern migration route was 547 miles, but this does not include any of the numerous deviations from the route and back tracks that the animals made. It also does not include movements on

136 the Serengeti Plain. In one drive around the Plain visiting the places occupied by major wildebeest concentrations during the wet season of 1961 we clocked 277 miles. The animals, however, were constantly moving during the several months they were on the central plains and it was not unusual to follow a herd 30 miles in one day, so the actual mileage covered by the herds on the plains is far more than 277 miles. Thus the minimum migration distance covered by the animals on the route that we followed would be 824 miles.

In 1960 there were two complete migrations between the Serengeti Plain and the Telek area of Kenya. Wildebeest involved in these movements who followed the direct route that we clocked would have traveled a total migration distance of 1,093 miles.

The northern "circle" has a maximum east-west spread of about 90 miles, and a north-south one of about 60 miles. The distance we clocked on our odometer following migratory movements during one cycle was 229 miles. This again is direct distance, not including additional mileage on the Loita Plain. In 1960 some of the wildebeests made two round trips to the Loita Plains in addition to the main cycle, so their yearlong migration distance total was 520 miles. These migration distances do not include the constant back and forth movements during the months

*136 the animals are on the plains, deviations, circlings, and back tracks while on the move, etc., hence represent a minimum distance covered by animals following the given routes.

(c) Localized Populations:

(1) Ngorongoro Crater: There appears to be a population of about 9,000 wildebeests living in the Crater. Various types of evidence would indicate that this population as a unit does not at present migrate between the Crater and the Serengeti Plain. The numbers of wildebeests within the Crater appear to be relatively constant throughout different seasons, even when there are large numbers of wildebeests on

and above, Numbers of Animals). In May, 1962, Mr. F.G. Waddington, Provincial Veterinary Officer, Tanganyika Veterinary Department, told me that earlier that spring a large number of wildebeests had been collected in the Crater and on the adjoining Serengeti Plain. Rinderpest antibodies were found in the blood of all the animals collected outside the Crater, while none were found in the blood of those inside the Crater. This would indicate that the animals within the Crater had not been exposed to the disease, while virtually all those outside had been so exposed (see below, Mortality).

*136 If this is the case, the two populations must have been separated, at least in recent years.

There is observational evidence, however, that some movement into and out of the Crater does take place. There is no topographical barrier to such movement. A series of prominent, wide tracks climb diagonally up the steep, 1,500 to 2,000 feet high Crater walls. These are the routes by which Masai with their livestock and some wild animals enter and leave the Crater. Several of these tracks converge at a low point on the west rim and lead through Windy Gap into the adjacent wide grassy basin called the Malanja Depression. The north edge of the Malanja Depression is a low, trail-notched limestone ridge, and from it there are about seven miles of rocky, grass and thorn bush covered slopes leading down to the Olbalbal Depression at the southeast edge of the Serengeti Plain.

Captain G.H.R. Hurst who had a farm in the Crater for several years after the first world war indicated that regular migrations in and out of the Crater occurred, noting that when conditions were dry outside the Crater the game population (in which wildebeests and zebras predominated) in the Crater was

#136 about three times larger than during the wet season when food and water were plentiful elsewhere (Joelson, 1928:210). In May, 1961, Mr. J. Newbould, Pasture Research Officer of the Ngorongoro Conservation Unit told us of meeting occasional groups of wildebeests moving up and down the slopes between the Crater and the Olbalbal Depression. Pearsall (1957:7) states that during November and December, 1956, "Several movements of wildebeests from the Ngorongoro Crater into Olbalbal and back were observed." Swynnerton had long experience in the region and described (1958:439) movements "over the western rim of the Crater down through the Malanja Depression and the western outer flank of the Crater to the Olbalbal..." As noted above, Grzimek and Grzimek do not believe that wildbeests from the Crater are involved in any such movement. They state (1960a:40) that although "There is no doubt that migration between Olbalbal and Malanja and back does occur ... there is no proof that the movement from Olbalbal to Malanja is extended to the Ngorongoro Crater."

We never observed wildebeests entering or leaving the Crater. However, on May 21, 1960, we counted [illegible] wildebeests in the Malanja Depression. Mr. [illegible] Menze, then Game Ranger at the Crater, wrote

*136(Grzimek and Grzimek, 1960a, footnote on p. 44) that "in late May, 1960 ... some 300-400 wildebeest had been observed in the Malanja Depression for some days. I saw them one evening forming themselves into a long file and trekking into the crater down the Windy Gap cattle track." On June 4 we returned and noted about 2,000 wildebeests again in Malanja. Neither we nor Mence (op. cit.) noted animals down the slope or on the then-dry adjacent Serengeti Plain. Therefore it appears that the 2,000 wildebeests we observed in Malanja moved into the Crater, part of this movement being observed by Mence, and shortly afterwards they climbed back out to Malanja.

From the foregoing it appears that there is some irregular movement into and out of the Crater by a significant portion of the normal wildebeest population, some of whom may reach the edge of the Serengeti Plain at Olbalbal. But in recent years there may not have been significant shifts in population or interchange of animals with the wildebeests from the plains.

*13 Within the Crater there is yearlong water. The fertile soil and abundant rainfall produce a rich grass cover. Consequently there would not

*13 appear to be any need for wildebeests living in the Crater to migrate out to seek food and water -- so long as their population and those of the other herbivores *136 remained in balance with the food supply. With a much higher population of wildebeests, however, migration or emigration might be necessary.

To examine this idea, one should know the carrying capacity of the Crater and the size of its past wildebeest populations. We do not know of any precise data available on either of these points, but there are indications. A number of estimates were made of the numbers of wild animals in the Crater in earlier years. The most conservative -- about 20,000 wildebeests -- is reported by a German, Dr. Hans Poeschel, who visited the area before the first world war (Grzimek and Grzimek, 1960a:37). Other estimates ran far higher. Captain Hurst (Joelson, op.cit.) "reckoned a minimum of 50,000 head (of all game) when food and water were plentiful elsewhere and three times that number in dry times..."

In 1961 the Tanganyika Game Department estimated the total wild animal population in the Crater to be the equivalant of roughly 12,000 wildebeest-sized

*136 (i.e. 400-500 pounds) animal units and the Conservation Unit placed the number of cattle then regularly grazing in the Crater at slightly over 3,000 and sheep and *13 goats at about 7,500 (Talbot, et. al., 1961:14). With this grazing pressure the Crater floor was overgrazed, although part of the trouble came from additional Masai livestock which were not taken into account in the above numbers which were moved into the Crater region due to drought elsewhere. A population of 20,000 wildebeests alone would exceed the present estimated total of all herbivores in the Crater, and with such numbers some need for migration might be expected.

*136 It is therefore possible that while at present there may be little or no significant migratory movement between the Crater and the Serengeti Plain, there were such movements in past times, especially if the population of herbivores in the Crater was greater.

(2) Ukerewe Peninsula - Ndabaka Plain: In May, 1961, we counted about 750 wildebeests on the Ukerewe Peninsula and about 4,200 more in the vicinity of the Ndabaka Plain (Fig.#2). These animals had not taken part in the previous season's main migrations and they had spent the wet season and dropped their calves in the roughly 1,000 square miles

*136 immediately north and east of Speke Gulf. These animals, or part of them, appear to represent a relatively localized population which does not take part in the main migration "circle." In some years the main migration from the Serengeti Plain reaches the Ndabaka area, and when this occurs there is probably some interchange of animals such as occurs when the Serengeti migration meets the Mara one. But there are no data on the size of the permanent Speke Gulf population nor on the extent of population movement into and out of the area.

*13 Weather in the Speke Gulf region is influenced by Lake Victoria, with high humidity and relatively high rainfall producing a yearlong grass supply. Perennial streams and rivers are abundant in the area, so presumably here as well as in the Ngorongoro Crater there is no need for a limited population of wildebeests to migrate far to obtain their required food and water. Small scale movements within the area do take place, however, and these, like the Crater movements, appear analogous to the larger scale migrations in the causal factors described below.

*136 Mr. Peter Ashard, former Game Ranger of the area, told us that formerly there had been regular

*136 movements of wildebeests between the Ukerewe Peninsula and the Ndabaka Plain area, but that he thought increasing settlement and agriculture in the area between them had stopped this movement. Further work needs to be done to define the movements and relationships of these populations.

(d) Non-Migrating Individuals: Constant movement is characteristic of most wildebeests, but there are a few individuals which are quite sedentary. In the Egolok area of the Kenya Mara about 30 old males remain throughout most of the year in restricted areas of a few acres each on hilltops. Their grazing, plus that of other animals -- especially semi-resident topis and migrating wildebeests -- keep the hilltop grasses low throughout most of the year. Perennial water is available usually within a mile, often within a few hundred yards of these territories. The hilltop drainage keeps the territories from becoming too muddy during the rains. The old males are undisturbed by humans. Most of the year these animals have water and preferred food available in the few acres each occupies. During part of the year, however, the grass does become dry but the animals usually continue to feed on it. If conditions become too dry the old bulls

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*136 will move a few miles but they return to their territories as soon as food is available again. We recorded them on their hilltops in every month of the year.

The only wildebeests that we have observed exhibit this solitary, sedentary behavior are old but apparently healthy males. Occasionally old males will remain for several months alone near water in other parts of the region, but none appear to be as permanent residents as the Egolok animals, one of which is reported by Major Temple-Borehame, Senior Game Warden of the Mara, to have lived on the same hilltop for over 13 years.

This solitary behavior occurs in Eastern Masailand also. Mr. S. Ellis and Captain D. Zaphiro have told us of such cases in the vicinity of the Nairobi National Park. Percival (1928) mentions examples in the Ngong Hills (near Nairobi) and the Rift Valley.

These old bulls do not display the typical wildebeests' reactions, described below, to social or other environmental stimuli. As a rule the older

*136 individuals' reactions to movement stimuli are less marked than those of younger animals and herds, but bulls display a gradient ranging from the responses indistinguishable from herd responses to those of the Egolok bulls. Darling (1960:25) also noted this difference between the behavior of individual and small groups of bulls and that of larger herds.

(e) Grass: As previously stated, wildebeests display a marked preference for short, fresh, green grass. In the present study, specific notes including location, movement, and activity were taken on 617,202 wildebeests.. Since the total population is around 240,000 wildebeests, we observed many of the same animals more than once at different times and locations. With the exceptions noted below these animals were all observed on, or moving in the direction of, areas of available short green grass usually in the proximity of surface water, or areas where it was raining or where rain had fallen within the past 24 hours. The exceptions were occasional dry season movements noted when rain, green grass, and surface water were temporarily unavailable, as discussed below.

Most movements of wildebeests were

*136 associated with the stage of growth of the grass. Areas of mature grass, or grass over about four inches in height were bypassed or left behind by movements to areas of grass that was just sprouting or was below four inches high. Short grasses of less preferred species were taken in preference to the preferred species, where the latter were mature and tall.

A relatively slight drying of grasses that otherwise appeared to be the preferred height and species apparently triggers some movements away from an area. This was usually observed on the central Serengeti and Loita Plains at the start of the dry season, when it would appear that the wildebeests were making an otherwise inexplicable movement off the plains, away from good grazing.

(f) Fire: Fire is of great importance to wildebeest movement and feeding. In no case have wildebeests been observed moving through thick, unburned brush, or very tall, unburned grass. We have watched migrating herds deflected by a strip of unburned tall grass only about 100 yards wide. In such a case herds of thousands of wildebeests would turn aside and move along the unburned edge until they found an

*136 open way through. Yet we have frequently observed wildebeests moving through brush so thick that a car had to force its way through or over brush and small trees to follow, when the brush had been burned previously and rain had brought up a carpet of short green grass. The determining factor appears to be visibility. A second factor may be the flush of new grass on a burn, although at least on open grasslands this would probably come with rain even without the fire (Heady, 1960).

(g) Rain: As noted above virtually every major population movement observed in the present study was associated with rain in the area toward which the wildebeests moved. Every movement away from an area of what appeared to be satisfactory feed was associated with rain in the area toward which the population moved. The animals would often leave a grassy area and move to a dry area where rain was falling; then stand or mill around there with no food for a day or two until the grass sprouts appeared. We have followed herds that moved up to 30 miles in one day, from an area of good food to an area where rain was or just had been falling. Then, after as little as 24 hours spent grazing on this area, the animals

*136 returned to the area from whence they had come where it was raining again. When the plains are drying in May or June, a mass movement toward the bush areas of over 100,000 wildebeests may be reversed by a heavy storm back on the central plains.

The wildebeests' reaction to rain becomes more pronounced as the grass and surface water dry up. When conditions are becoming drier, individual animals and herds exhibit increasing restlessness and a small, relatively distant storm will trigger movement, while under wet conditions such a storm would probably produce no reaction.

(h) Follow the Leader: Movement and proximity of other wildebeest herds also appear to influence individual wildebeest's movements. Individual animals or small herds that have occupied an area some days or weeks are often picked up by a passing herd. Smaller herds or individuals moving in one direction will usually shift direction to follow a larger herd. Any group of wildebeests will tend to follow animals -- wildebeest or otherwise -- moving in a determined way and/or moving rapidly.

19: Talbot E-4,5 (1956-1962)1964 FL12 Masai FL12

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Scent deposited by the pedal glands as well as sight may trigger the follow the leader behavior. After a large herd of wildebeests has passed, the scent from their pedal glands is often so strong that a human can follow the herd by it. Migrating wildebeests often walk in long, single lines, with other herds following the same lines some hours later. Apparently the later animals are navigating by the scent, just as we did following herds through thick brush; and they may also have been influenced to follow the herd in the first place by the scent.

The response of an individual wildebeest to the various movement-producing stimuli is greatly influenced by the herd. In this respect wildebeests are similar to caribou, but quite different from mule deer whose movements are apparently motivated by individual stimuli affecting every deer independent of the rest (Leopold, et. al., 1951).

(1) Wet Ground Surface: Patterns of grazing intensity and observed animal movements on various plains areas are not correlated with the species of grass present, where this is constant, but rather with the available grasses that were growing on

*136 the driest footing. In 1959 Dr. Harold Heady suggested to us as an explanation for uneven grass usage patterns that wild animals might avoid wet black cotton soil, as it balled up on their feet. During the present study, in no case where they had any apparent option to do otherwise did wildebeests enter or cross muddy black cotton clay patches. The result is a very irregular pattern of grazing during the wet seasons, with the higher areas getting intensive grazing while the swales and bottoms are left to grow tall and rank. *Areas of preferred grass at the preferred stage of* growth are often by-passed by moving, grazing herds, if the surface is muddy. Left ungrazed for several days during the period of peak growth the grass may grow beyond the preferred stage of the wildebeests. Later these ungrazed areas appear as islands of undesirable grass in an other wise heavily grazed area. Yet we have observed these same areas very heavily grazed by the wildebeests in another season when the grass was at the right growth stage and the soil was relatively dry.

(j) Dry Season Conditions and Permanent Water: Certain movements of wildebeest populations occur which cannot be associated with rain storms or green grass, as they take place in temporarily rainless

*(36 periods of the dry season, in areas totally devoid of any short green grass. Such movements fall into two catagories:

(1) *Aimless Wandering*: A large herd, numbering many thousands of animals, must keep on the move even under conditions of good grazing merely because the grazing pressure is so great that they exhaust the forage in one spot very quickly. Some movement, then, is characteristic of any large concentration of wildebeests. During dry periods when little or no fresh green food is available and no rains are visible, large herds mill about, usually in a more or less circular pattern, often moving back and forth from one source of water to another. Such movements are fairly characteristic of the dry season behavior of herds between the Grumetti or Orangi Rivers and the Mbalangeti River in the western Corridor of the Serengeti Park, and judging by the depth of the game trails which they follow moving back and forth, this pattern has held for many years.

(2) *Oriented Movement*: When the wildebeests are on the open plains and preferred feed and water become unavailable, a movement *away from* the

*136 plains takes place. There is no single "migration route" off the plains, instead there is movement which may be concentrated or widely dispersed, eddying and flowing around obstacles through the bush country to the watercourses. Animals in the north or east of the Serengeti Plain generally move north, while those in the south, center or west of the plains usually move west or northwest. Game trails worn deep into the soil lead from the plains to the nearest water supplies. Generations of wildebeests appear to have used these water points in dry seasons coming from the different areas of the plains. It appears reasonable to us that this otherwise apparently unguided movement off the plains reflects knowledge of the location of permanent water, and this knowledge controls movements in the absence of stimuli such as localized rain, which would otherwise provide direction for movement. This knowledge would be learned, just as a dairy cow learns her pasture and a sparrow his home range. Such knowledge would also help explain other oriented movements in the dry season which occur without obvious external stimuli.

*13 The location of "permanent" water, as well as food, changes through the dry season. In dry

19: Talbot E-4,5 (1956-1962)1964 FL12 Masai FL12

*13 years, water can be found in different watercourses, or different parts of the same watercourse, at different periods of the dry season. For example, early in the dry season there is ample water in and near the upper reaches of the Telek River (ir Kenya), but later water is only found in scattered pools near where the Telek joins the Mara River. On examination, the generalized migration routes or circles described above appear logical in view of the probable location and period of availability of food and water in the dry season.

*136 In Kenya, for example, after leaving the dry Loita Plain the wildebeests move southeast toward the Egolok region. Their route follows early dry season water in the upper Telek River and its tributaries, expecially those from the Sianna Hills. During the dry period depending on rainfall, burning, etc., the animals move back and forth in an area where water is periodically available from the Telek, Jagatiak, Sand, and Bologonja Rivers; but during the driest periods, the wildebeests move to the low lying grasslands along the Mara River, the one major perennial watercourse on the Kenya side. When rain falls farther east the wildebeests leave the Mara River and move

*136 east and north, where temporary water is available on the greening Aitong and Bardamit Plains, until they reach the then-wet Loita Plain.

In Tanganyika, the generalized route for the animals that move off the plains in a westward direction takes them past the early dry season grazing around the headwaters of the Simiyu and Duma Rivers and down the Mbalageti. They then graze on the plains areas between the Mbalageti, Grumeti, and Ruwana Rivers, eventually moving northeast up the drying Grumeti and Ruwana Rivers and their tributaries, toward the truly perennial waters of the Mara and Bologonja Rivers. They sometimes then follow down the Tabora River to the Mara, proceeding up the Mara and then eastward along the Bologonja; when it rains to the south they head back southward down or past the upper reaches of the Grumeti, Rokari, Bololedi, Mgungu, and Orangi Rivers to the Serengeti Plain.

*13 Rainfall, burning, and available grass and water vary greatly from year to year. The critical years are the especially dry ones, when for long periods there are no storms to follow, and in such years these generalized routes appear to keep the

#13 animals in the vicinity of most probable water and #156 food. Following the routes, then, could be a learned response that occurs when no obvious external stimuli are present.

It is emphasized, however, that these movements do not constitute what appear to be a single, fixed migration route. The variability of these movements is illustrated by the general routes taken by the main concentrations of wildebeests leaving the Serengeti Plain during the past three years. In 1962 a major concentration of wildebeests reached the northern edge of the plains near the park boundary (Fig. 8). The previous year the major concentation left the central plains in the west at the Simiyu River. In 1960 the main concentrations followed a general course between those of the two subsequent years, passing Seronera Camp at the northwest corner of the plains.

The timing of the movements away from the plains also varies, of course, depending on the weather. In recent years the dates when the major concentrations first reached the edge of the plains have ranged from May 3rd (1960) to June 20th (1957).

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(b) Location of "Calving Grounds:"

"Traditional Calving grounds" have been mentioned in the literature (e.g. Swynnerton, 1957) as a factor possibly influencing migrations, and this was a possibility frequently mentioned to us by people in East Africa. We have no evidence, however, that the movements of wildebeests are influenced by any desire or intent of the wildebeest cows to drop their calves in any particular place. The calves are dropped wherever the cows are at full term and the cows' locations are determined by the migration stimuli discussed in this chapter. Calves may therefore be dropped virtually anywhere in the region, depending on that season's patterns of burning and rainfall which determine the wildebeests' movements.

With few exceptions wildebeests drop their calves between the third week of November and the second week of May, with most born in January and February. Under what are considered "normal conditions" by persons in East Africa who are acquainted with the Serengeti-Mara region, most of the migratory wildebeests will be on the Loita and Serengeti Plains during this period. But conditions vary greatly, and in the Mara, for example, in 1960 and 1961 nearly

*136 as many calves were dropped in other parts of the area as were dropped on the Loita Plain proper.

(1) Migration Stimuli: The sense of smell is doubtless important in some cases, as when a herd approaches a water point or when it happens to be down wind of a rain storm. However, over half of the observed movements of wildebeest in the direction of rain were cross wind or down wind, where there was no possibility of scent playing a role. Smell also appears to aid wildebeests to follow other wildebeests, and it may be an important part of social stimuli.

Hearing may be important in some cases. As an illustration, we have observed a feeding wildebeest herd on the open plains when a thunder storm occurred about 15 miles away. At the first thunder the animals raised their heads and looked around. There was increasing activity in the herd for about 30 minutes, then the herd began moving in the direction of the rain. In other cases the thunder may be the sole means by which a herd out of sight or scent of rain learns of its presence. It is not uncommon for a herd to move toward rain when the actual storm was not apparently

136 visible to the animals, and when the wind was from them to the rain. We have seen several such examples, and Brooks (1960:14) described an instance where wildebeest and Thomson's gazelle were on the *far* side of a ridge which rose 3,000 feet above a plains area where it rained. "...By the next day green grass had appeared where the rain had fallen and simultaneously a herd of 500 tommy and an equal number of wildebeest arrived. ... How did they find or sense the fresh grass when they were out of sight?"

Sight appears the primary sense involved in wildebeests' movement when associated with rain. Except in the middle of the wet seasons, rainfall in the Serengeti-Mara region is local and irregular, and usually consists of heavy localized storms visible as dark, cloud capped columns for distances of over 50 miles. Most observed wildebeest movements were in the direction of such storms. which were quite visible to the observer (who was with the wildebeests).

We observed several instances where herds of wildebeests appear to have been led astray by mistaken location of an observed rainstorm. Two such

*136 cases occurred in the Kenya Mara region. In both cases, during the dry season, herds of up to 3,000 wildebeests moved from the Mara River or Telek region of perennial water, up across the Bardamit Plains to the Loita Plain. These movements coincided with very heavy thunder and rain storms near the Loita Plain, which appeared to be on the Loita Plain and which we saw and heard while we were with the wildebeests at the time. The rain had fallen not on the plains but on the nearby wooded hills. The wildebeests in both cases milled about on the dry plains for about two days, with no water and apparently no suitable food. Then they returned the way they had come, moving at a steady trot 60 miles to the rivers that they had left. The total distance covered in each of these apparently futile round trips was roughly 120 miles.

The importance of what appears to be knowledge of topography and water sources in navigation, i.e. orientation of migration movements, was discussed above. Learning also appears to affect wildebeests' reactions to external stimuli.

Visible rain falling outside the normal

*/136 range of the population (e.g., on the Siria Escarpment) may cause some restlessness in wildebeest herds in the region, but it apparently does not trigger any movement. We believe this is the result of a learning process, at least partially expressed through what we call herd tradition. If we postulate that it is possible for wildebeests to learn the location of permanent water and of barriers to movement (escarpments, wooded mountains, etc.), then most adults in a wildebeest herd will not start toward an unreachable goal. The influence of the herd upon the individual wildebeest is very strong. Those individuals that have not learned the location of a barrier probably will not react to the stimulus of rain falling beyond that barrier if the herd does not react to it.

Changes in humidity might be another stimulus involved in initiating some wildebeest movements, especially the departure from the central plains. As noted above, wildebeests are more sensitive to migration stimuli during dry conditions than during wet. The sensitivity may be affected by water or nutritional stress or humidity, or more likely, a

*136 *[126] combination of these factors. We carried an hygrometer during part of the time that we followed the wildebeests, and on the basis of its readings we were unable to correlate humidity alone with movement. However, we could rarely get readings before and after movements. [128] More satisfactory data on this problem could be obtained by recording hygrometers located on the plains and at other key points on the animals' migration routes.

*136 128 Since the study area is virtually on the equator, day length is constant yearlong and hence can not be a migration stimulus. Location of the sun and stars might be involved in navigation, but they probably are not involved in initiating migration, since the timing of migratory movements varies so much.

*136 Conclusions and Summary: Wildebeests remain on open grass plains during the wet seasons, and when the plains dry they leave, eddying and flowing through the surrounding bush country following preferred food and water. There is no single fixed migration route. Instead there is irregular

*136 movement dispersed over a wide area, unless rainfall pattern and topography temporarily concentrated a mass of animals. In the 12,000 square mile area of study there are two main migration patterns, both very roughly circular and clockwise, one of which may involve about 800 miles of travel, based on the Serengeti Plain, and another of about 300 miles based on the Loita Plain. These migrations sometimes join near the Kenya border and interchange of population takes place. Not every area is visited each season and movement along specific routes is dependent upon patterns of rainfall and burning. Smaller wildebeest populations are localized near Speke Gulf and in Ngorongoro Crater. The Ngorongoro population at present appears largely isolated from other migrations, and the Speke Gulf one is partly so.

The movements of wildebeests appear determined primarily by the availability of grass at the right stage of growth, and surface water. Particularly wet and muddy surfaces are avoided. Fire is an important factor in clearing areas of rank, tall grass otherwise avoided by wildebeests, and possibly in stimulating or making available fresh grass growth.

*136 Rainfall, detected by visual, auditory or olfactory senses, triggers most wildebeest movement; where no rainfall nor fresh grazing are available, knowledge of topography, including permanent water sources appears to determine movement. Wildebeests are more sensitive to migration stimuli in dry or drying conditions than in wet.Singles and small herds of bulls are less sensitive to social and environmental stimuli than females and larger herds. Individual response to movement stimuli is strongly influenced by herd behavior. Movement is highly erratic, depending as it does largely on localized rainfall and burning.

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Reproduction

*136 The reproductive cycle of each species appears closely correlated with the species' nutritional requirements and habitat conditions. The young are born at the time when environmental conditions are most favorable for their survival. Wildebeest calves are born between late November and early May, with a peak in January and February. This period is correlated with the rainfall regine, as described above, and coincides with the highest probability of an abundance of fresh grass of their preferred species. Thus the cows should be on a high plane of nutrition.

*[132] Normally the rains continue into May assuring that the preferred sources of nutrition for the wildebeests will be available through the period of calving, early calf growth, and rut. After early May as the dry season progresses the animals lose condition, young calves have less chance of survival, and cows bred while in poorer condition have less chance of producing young that will survive.

Success in reproduction in species of wild and domestic ungulates appears determined primarily by the plane of nutrition of the animals before and during the rut (Buechner, 1960; Cheatum and Severinghaus, 1950;

*136 Hart and Guilbert, 1933; Jones, 1955; Miller, et. al., 1942; Morton and Cheatum, 1946; Taber, 1953; Taber and Dasmann, 1954, 1958). Ovulation may be delayed or prevented by a low level of nutrition, particularly by a deficiency of Vitamin A and protein, as described, among others, by Hart and Guilbert (op.cit.) and Miller et. al. (op. cit.). Other effects of such a deficiency noted by these and other workers are pre-natal mortality and the birth of weakened young which may die soon after parturition.

Topis have a limited calving season with a peak about October, which would appear to be correlated with the availability of grasses at their preferred growth stage. Zebras and Thomson's gazelles produce young throughout the year with a peak in the long rains. Grant's gazelles, having very low free water requirments and feeding on dry, low protein food, produce young throughout the year but mostly on the drier plains.

Most wild ungulates of the study area have an extremely high reproductive potential. As an example, over 90 per cent of all wildebeest cows over one year of age are bred and produce a calf annually. Similarly, most of the other antelopes appear to produce at least

*136 one calf per female of breeding age per year.

Mortality

For this discussion we are concerned with mortality as a limiting or balancing factor in the ungulate population of the ecosystem. The primary terminal causes of mortality are predation (by human and quadraped predators), disease, and accidents. Environmental stress of some sort (such as drought) may weaken animals and be the underlying cause of mortality. An animal weakened by drought could be easily killed by predators which would not attack it if it were healthy.

The primary predator in Western Masailand is the lion. We estimated that an individual lion would kill about 35 prey animals a year, on the basis of two kills a week for an average pride of three animals. Wright (1960) believed the average annual kill per lion was 36.5 prey animals. Roosevelt (1910) estimated an annual kill of about 52 to 73 prey animals. Major Temple-Boreham (Kenya Game Dept., 1950) estimated about 52 prey animals killed annually by each lion. Thus, the average annual kill per lion appears to be between 35 and 52 prey animals.

Our estimate of the numbers of lions in the study

*136 area was about 700. Using the above figures, the average annual prey kill by lions then would be from 24,500 to 36,400, or somewhere between two and four per cent of the total ungulate population.

Other predators include leopards, cheetahs, wild dogs, jackals and hyenas. The first three are not present in sufficient numbers to much affect the prey population, and a large part of the food of the latter two forms is provided by lion kills. Consequently, predation by wild animals is not now a limiting factor on the ungulate population as a whole.

As noted above, poaching has been considered an important limiting factor, and it may have been in the past. Evidence at present indicates that it is not of much importance. Disease does not appear to much affect the numbers of wild ungulates in the study area, except for the wildebeests. "Yearling disease" which appears to be a combination of rinderpest and environmental stress kills a large number of wildebeest calves when they are about seven to ten month old (Talbot and Talbot, 1963b). Accidents account for some adult animals in large herds. Figure 46 and 47 illustrate the observed mortality of wildebeests in the study area.

*136

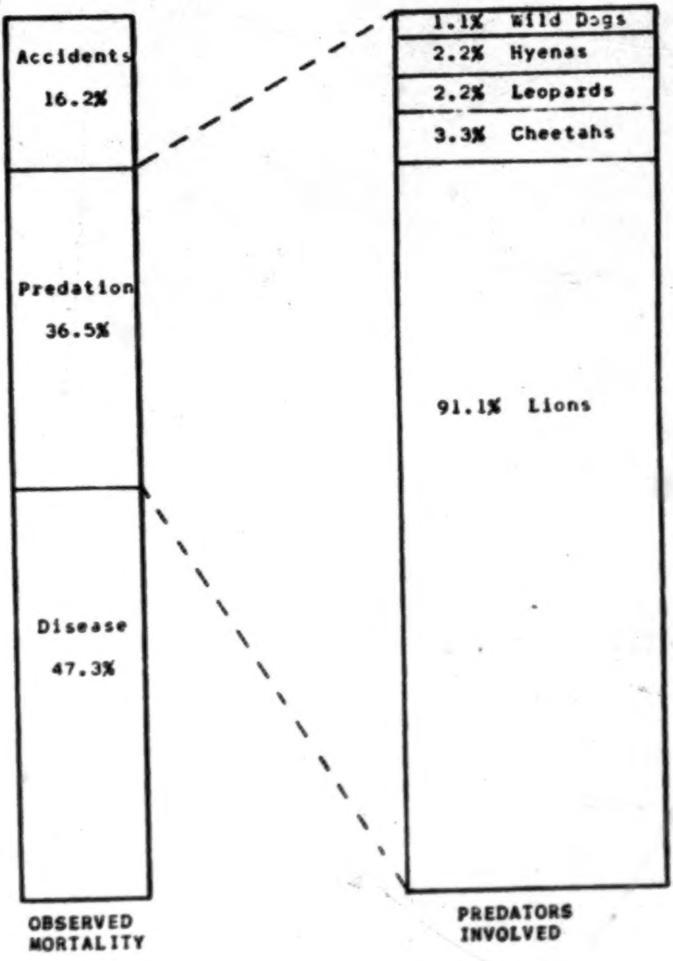


Figure 46.

Primary Causes of Observed Mortality, and Predators Involved in the Serengeti-Mara Wildebeest Population.

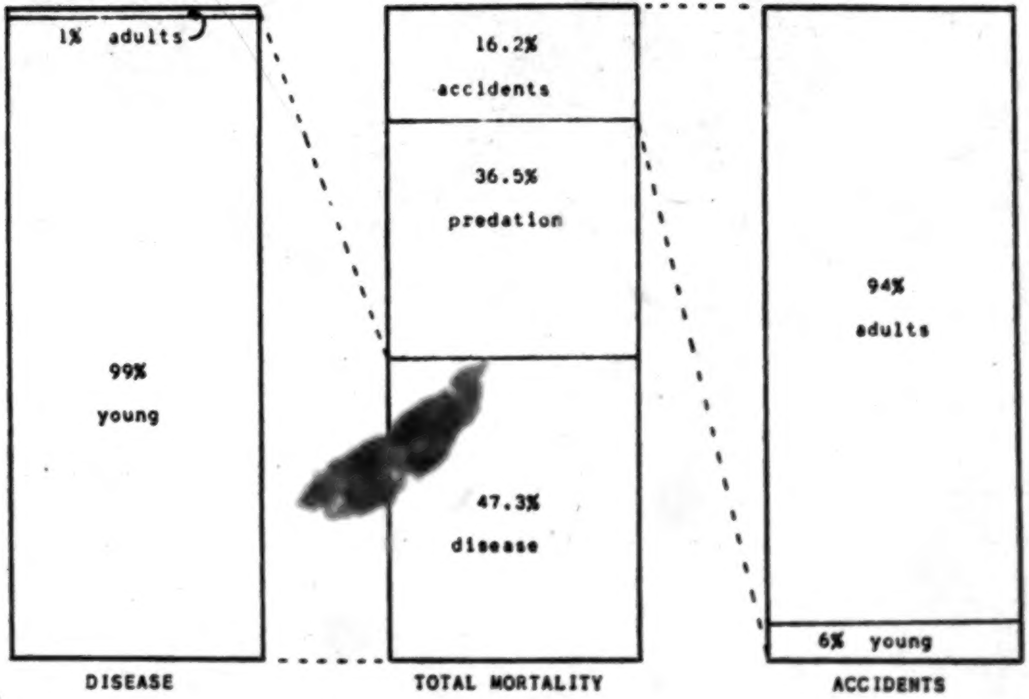


Figure 47. Age Distribution of Observed Mortality Caused by Disease and Accidents in the Serengeti-Mara Wildebeest Population.

*136

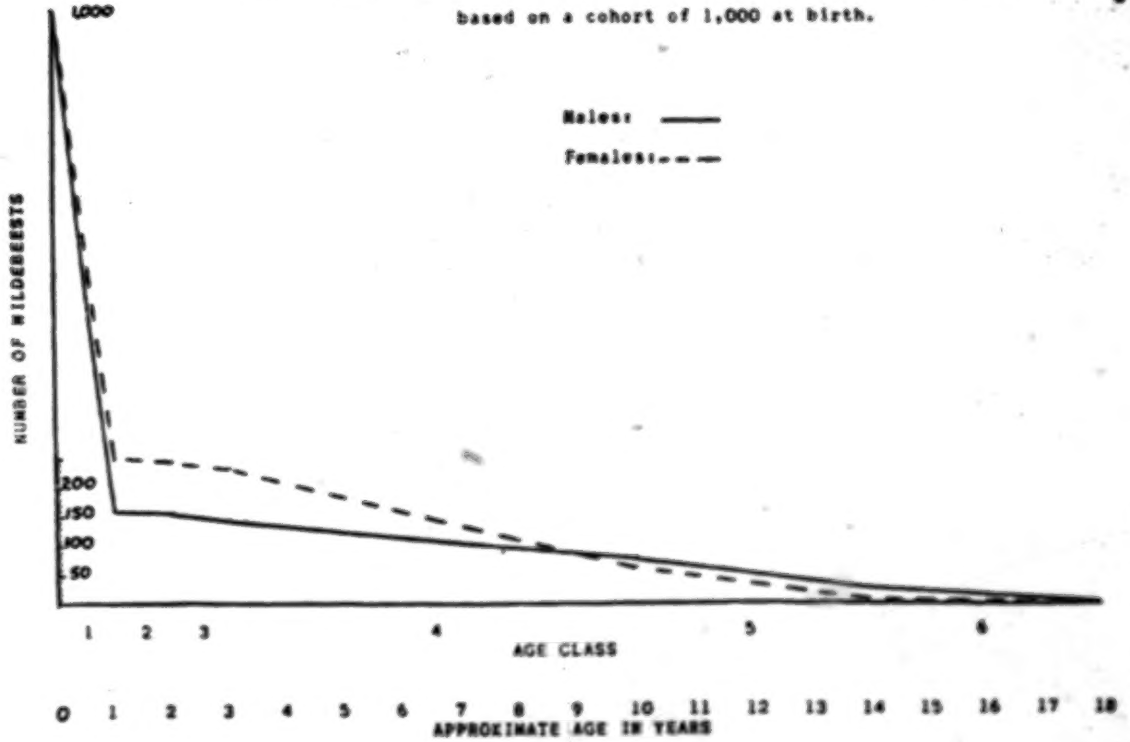
*136 In aggregate, the animals killed by the above factors -- predation, disease and accidents -- do not come near the numbers of animals that are born into the ungulate population. There must, therefore, be some other limiting factors. In the case of the wildebeests, the age structure of the population (Fig. 48) shows that the greatest mortality is in the calf population during the first few months of life. The mortality here is caused primarily by cows becoming separated from their calves in the milling-about of large herds. This is a function of herd size, the larger the herd the greater the loss of calves. The size of herd is influenced by a complex of environmental conditions, described in detail in Talbot and Talbot, 1963b. Thus, the primary limiting factor in the wildebeest population appears to be environmental, acting through herd size.

It would appear that with other species also, the effective limiting factors involve environmental controls of one kind or another, or, in effect, the carrying capacity of the grassland ecosystem. This is not
[224] necessarily a self-regulating system, however. The
[178] balance that formerly existed included native hunting. This now has been largely stopped. One result of this protection has been the increase in giraffes. In the

[TEXT CONTINUED ON PAGE 309]

Figure 48 Age Structure of the Serengeti-Mara Wildebeest Population

based on a cohort of 1,000 at birth.



*136

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

19: Talbot E-4,5 (1956-1962)1964 FL12 Masai FL12

#136 Mara giraffes have been effectively protected for about 15 years. According to personal accounts, they have
#13 increased greatly in numbers. The appearance of the vegetation confirms this belief. The trees preferred by the giraffes have a grazing line about 20 feet up. Virtually no green leaves exist below the line, although there are many dead or leafless limbs lower, indicating that in the recent past leaves did grow lower. Almost no reproduction of the preferred trees can be found.

#136
178
224 Elephants are another example of a species formerly limited by hunting, and increasing with that cause of mortality removed. They have been protected along the Mara River since about 1900, and by 1928 the increase in their numbers was notable (Kenya Game Dept., 1928). This increase has continued. It is due in part to natural increase within the area, and part to immigration from outside areas where hunting is allowed.
#[137] Tree destruction by elephants is significant in the area and was obviously increasing.

An increase in the populations of giraffes and elephants is readily apparent because of their obvious impact on the landscape. Such increases on the part of other smaller ungulates would be much harder to detect without periodic accurate censuses. There has only

136 been one overall accurate census of the region. Indirect evidence of increases in the numbers of smaller ungulates
13 would come from overgrazing. The areas most heavily
231 overgrazed are those grazed by domestic livestock.
233 In Kenya the areas not available to domestic livestock do not show overgrazing, but in parts of Western Masailand in Tanganyika there is local overgrazing in such areas.

136 As discussed above, the predation at its present level does not appear to be a limiting factor. In past years, however, the predator populations were far higher. Wild dogs are rare in the area at present. We estimated their population at between 75 and 150 for the entire Western Masailand. For years it has been the custom of white hunters and many game and park wardens to shoot the animals. Monty Moore, the game warden who lived at Banagi in the 1930's, killed every one he could, and told of one case where he killed 50 out of a pack of 53.

Lions were considered vermin until recent years and literally thousands were killed. As noted above, almost 300 were legally killed in the Mara between 1946 and 1948. Individual hunters such as S.E. White could and did without dozens. One Californian, L. Simson, is reputed to have killed 287 lions (White 1926) and except for the marksmanship involved, this was not thought out of the ordinary. Legal hunting continues around the periphery of Western Masailand, and lions are killed when they wander out of the parks and bother African cattle.

Consequently, it is probable that in times past there were far more major predators in Western Masailand than there are now. As a result of lowering the human and animal predator pressure, the ungulate populations may be increasing.

19: Talbot E-4,5 (1956-1962)1964 FL12 Masai FL12

*13

UNGULATE BIOMASS

For calculations of biomass, we obtained the numbers of animals and their sex and age ratios as described above. The weight data from our own work and that of our cooperators enabled us to establish average figures for males, females, and various age groups in the populations and to use these specific weights -- instead of arbitrary averages -- to determine biomass.

Table 25 presents the yearlong biomass data for the study area. The actual ungulate habitat within the study area covers about 10,660 square miles. Of this, about 3,144 square miles are open grassland and 7,515 square miles are bush. There is a relatively low population of animals resident in the bush country, including elephants, buffaloes, impalas, waterbucks, giraffes, rhinoceros, and some topis and kongonis.

The yearlong biomass from these animals is about 3,008 pounds per square mile. The bulk of the wild animals are migratory, and these include Thomson's gazelles, wildebeests, zebras, elands, and some topis and kongonis. There animals spend the wet seasons in the open grasslands and the dry seasons in the bush. Domestic livestock, Masai cattle, goats, sheep and donkeys also graze the

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231
*233

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Table 25. YEARLONG STANDING CROPS OF DOMESTIC LIVESTOCK AND WILD UNGULATES IN THE SERENGETI-MARA STUDY AREA

Type of Range	Approximate Area square miles	Animals	Approximate Yearlong Standing Crop pounds / square mile
Grassland, savanna, and bush	10,700	12 wild ungulates(2) 4 domestic ungulates(3)	30,200(2)
Bush	7,500	12 wild ungulates(2) 4 domesic ungulates(3)	23,300(2)
Open grassland	3,150	8 wild ungulates(2) 4 domestic ungulates(3)	46,800(2)
Savanna(1)	1,000 - 2,000	12 wild ungulates(2)	70,000 - 100,000(2)
Bush(1)	2,000 - 3,000	12 wild ungulates(2)	30,000(2)

(1) Ungrazed by domestic livestock, generally within about five miles of water.

(2) Fifteen additional species of ungulates are present in the area, but they are either smaller or rarer than the 12 included and their numbers are not known, so their biomass is not included. Therefore the biomass figures as given are low.

(3) Cattle, sheep, goats, and donkeys grazed by the Masai tribes.

*13 231 *235 open plains during the wet seasons. Some of them follow the wildlife into the bush country during the dry seasons, and some leave the region, moving to grazing lands in *13 the adjacent highlands. For roughly six months each year the open grasslands support a biomass of about 93,545 pounds per square mile, and for the remaining six months they are virtually empty of ungulates. The yearlong average biomass, then, is about 46,773 pounds per square mile.

During the six dry season months the bush country supports a biomass of 37,549 pounds per square mile, made up of the migratory animals plus the few resident ones. The average yearlong biomass in the bush country is about 23,299 pounds per square mile.

*13 231 *235 The overall average yearlong biomass, i.e. the weights of the average wildlife and domestic livestock populations divided by the square miles of the area, has been 30,214 pounds per square mile of which 80.2 per cent is wildlife and 19.8 per cent domestic livestock(1)

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(1) These figures refer to conditions up to about 1960, when livestock was removed from part of the area in Tanganyika through changes in regulations affecting grazing.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

#13 These overall figures, however, do not necessarily reflect the true carrying capacity of the landscape. Much of the area provides virtually no food for the ungulates, and serves largely as areas of transit, travel routes. Other areas, especially those within about five miles of reliable water supplies and those not grazed by domestic livestock, support extremely high yearlong biomass. In the realtively well watered savanna country midway between the vast open grasslands and the true bush the yearlong ungulate biomass ranges from around 70,000 to 100,000 pounds per square mile, and even in the bush country, within about five miles of water the yearlong average is well over 30,000 pounds per square mile. There is no evidence of overgrazing with these stocking rates.

#13
231
#233 The average biomass obtained from cattle, goats and sheep under native herding is about 11,000 to 16,000 pounds per square mile in the equivalent savanna, and 2,000 to 8,000 pounds per square mile in the bush. Under this degree of grazing intensity the habitat shows evidence of moderate to severe overgrazing.

#13 An even more striking comparison can be made with European cattle ranches in equivalent high savanna. In these areas, with careful management including fencing

*(3 nd provision of water points, the average biomass is ,000 to 32,000 pounds per square mile (Ledger, et. ., 1961), a third to a fifth of that obtained by managed wild ungulates. Even in these areas evidence overuse is the rule.

Table 26 compares biomass figures from the udy area with those from wild and managed populations other parts of the world. It is not a complete view; only a few representative examples have been osen. Weights are based on data provided by the ferences involved.

The biomass of mixed wild ungulates in Western ailand is very high relative to the biomass of estic livestock on equivalent lands in East Africa, well as to that of other wildlife populations in er parts of the world. When undisturbed this East ican wildlife does not overgraze and lower range ductivity, while existing domestic livestock grazing East Africa usually does.

The factors contributing to this biomass include complementary diets of the various ungulate species, nutritional efficiency of the animals themselves.

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*13

Table 26. YEARLONG UNGULATE BIOMASS DATA FROM EAST AFRICAN STUDY AREA AND ELSEWHERE

Approximate Yearlong biomass lbs./sq. Mile	Approximate Size of Area Square Miles	Animals	Range Type	Location	Reference
70,000-100,000	1,000-2,000	Wild ungulates	Savanna	East Africa	This study
30,000	2,000-3,000	Wild ungulates	Bush	East Africa	This study
26,700	......	Domestic livestock	Average of virgin long and short grass	Western U.S.	Watts et. al.
14,000-20,000	......	Bison & associated wild ungulates	Prairie	U.S.	Bourlière, '61; Petrides, '59
19,700	1,126,500	Domestic livestock	Average of all virgin ranges	Western U.S.	Watts et. al., 1936
10,600	......	Black-tailed deer	Managed chaparral	California	Taber & Dasmann, 1958
6,900	......	Black-tailed deer	Average of oak woodland plus chaparral	Pacific Coast N. America	Taber, 1961
5,800	2	White-tailed deer	Woodland proper density	Michigan	O'Roke & Hamerstrom ,'48
3,550	4,373	Red deer	Deer Forest	Scotland	Lowe, 1961
1,360	88,080	Mule deer (5 races)	Average all ranges	California	Longhurst, et. al., 1952
1,300	......	Mule deer	Average all ranges	Arizona	Swank, 1958

*13 and freedom of movement over a large area which allows the migratory wild animals (which make up the larger part of the biomass) to seek out their preferred plant species at the preferred stage of growth.

VEGETATION

Methods

*126 Much information on the vegetation was obtained from the observational methods discussed above. The *114 field transects were of particular value. We profited *122 greatly from preliminary visits to the study area with *126 Dr. Harold Heady of the University of California, Dr. P.E. Glover, Kenya Department of Veterinary Services, and Dr. P.J. Greenway, East African Herbarium. From these experts on East African vegetation we received our foundation knowledge for plant identifications in the area. In addition plant collections were carried out throughout the area which were identified by personnel of the East African Herbarium.

*125 To determine the species composition and other *126 information about grasslands we made a series of vegetation transect plots. The base method used was a step point or toe point transect. This was the method used by Dr. Heady on his grassland studies in East Africa. He advised that we use it for our study and kindly instructed us in its procedure. To determine species composition we identified 200 to 400 points on each plot identifying the plant rooted nearest to the point. In addition we used a quarter meter grid, centered on

*125 each 15th point, to estimate basal and crown cover. The *126 plot was photographed and detail notes were taken on the site and its use, fire history, etc., and all data were recorded on the vegetation plot check sheets (Fig. 49). Soil samples, described above, were often collected in connection with these plots. The plots were also frequently made where animals were collected to compare the available food with what was in the animals' stomachs. Plant collections were made on each plot site and were later identified at the East African Herbarium.

We made 70 such plots throughout the study area and several times that many additional plots where collections were made and the vegetation described, but a minimum of 200 points were not identified.

To help analyse the effects of fire on various vegetation types we made a series of burn plots. Information of the effect of the burn on various types of vegetation and ground cover, and data on regrowth were recorded on the burn plot check sheets (Fig. 50).

The preliminary check list of grasses (Fig. 51) that we compiled in October, 1959, included 72 species that we had found records of from the study area.

Subsequently we greatly enlarged the list, but the

Subsequently we greatly enlarged the list, but the

(TEXT CONTINUED ON PAGE 324).

Figure 49.

*125

CHECK LIST FOR __VEGETATION PLOT__

PLOT NUMBER .... Photographs: Roll no.............
Locality: Exposure no........
Notes:

Date..................... Time............

__Weather__ clear; scattered clouds; overcast; showers; rain; breeze; wind;
Last rain/shower ......days ago; past week; month; other
Notes:

__Habitat.__

__Association:__ grassland; grass-scattered bush; grass-scattered trees; forest; scrub; marsh; riverine; other.

__Site description.__

__Stage of growth:__ most vegetation: sprouting; flush growth; flowering; seeding; dormant; dry; dead; notes:

__Fire history__ burned in: past week, month; year; no evidence of fire;
Notes:

__Elevation:__

__Topography:__ flat; rolling; gentle slopes; steep slopes; plains; plateau; valley; ravine; irregular;

__Exposure__ Level, N.; E.; S.; W.;
full sun; partial sun; open shade; deep shade;

__Slope.__

__Drainage:__ well drained; impeded drainage; marshy; standing water; running water;

__Soil__ SAMPLE NUMBER.........
sand; rock; sandy; black cotton; other.

__Horizons__ A B C

__Surface__ loose; duff; Notes:

__Moisture.__

__Utilization.__ grazed; browsed by wildlife. species
by stock: cattle; goats; sheep

__Intensity:__ light; intermediate; heavy

__Insects.__

__Plant cover__

__Total.__ ....

__Grass.__ ....

__Notes.__

__Species Composition.__........................ ....
....
....
....
....
....
....
....
....
....
....
....
....

L. M. Talbot
Serengeti-Mara Wildlife Research Project
c/o E.A. Commission, Nairobi, Kenya, East Africa
October 1958

125

Figure 50.

L.M.Talbot
Wildlife Research Project
September 1960

BURN PLOT

Number...... **Photo Roll** no..........Exposures...........Direction.......

Description:

Locality:

Date: Time: **Plot Description:** strip; quadrats; area........

Site Description:

Elevation: Association:

Species Composition:

Topography:

Exposure: Slope:

Soil **Soil sample no**...........

Moisture:

Fire Data:

When burned: Previous burns

Size of burns

Intensity:

Effect on Vegetation:

vegetation		% burned	% unburned killed	% leaves withered, not dead	% unaffected	Remarks
Grass						
Weeds						
Brush	0-3'					
trees	3-6'					
	0-3'					
	3-6'					
	6-12'					
above	12'					

Notes, differential effect on species:

Ground Cover Remaining:

	Grass	Weeds	Brush	Trees	Total
Basal					
Crown					

Duff:

Humus:

Rain since burn? yes, no. When:

Regrowth	**inches high**	**Species**	**Notes**
Grass			
Weeds			
Brush			
[illegible]			
Trees			

Succession and conclusions:

*125

Figure 51.

PRELIMINARY CHECK LIST OF THE GRASSES OF THE SERENGETI-MARA
Compiled October, 1959

PLOT NO. ______

Andropogon sp.

Aristida adoensis
" adscensionis
" kerstingii
" keniensis
" sp.

Bothriochloa insculpta
" pertusa
" radicans

Brachiaria brizantha
" sp.

Cenchrus ciliaris

Chloris gayana
" pycnothrix
" sp.

Chrysochloa orientalis

Cynodon dactylon
" plectostachyus

Dactyloctenium sp.

Digitaria [illegible]?
" macroblephara
" milanjiana
" scalarum
" ternata

Echinochloa haploclada

Enteropogon macrostachyus

Eragrostis aethiopica
" braunii
" [illegible]
" cilianensis
" exasperata
" [illegible]
" [illegible]
" tenuifolia

Eriochloa nubica

Eriochloa nubica

Eustachys paspaloides

Exotheca abyssinica

Harpachne schimperi

Heteropogon contortus

Hyparrhenia filipendula
" lintonii
" sp.

Loudetia kagerensis
" simplex

Microchloa kunthii

Panicum coloratum
" deustum
" [illegible]
" infestum
" [illegible]
" [illegible]
" poaeoides
" sp.

Pennisetum [illegible]
" stramineum

Setaria incrassata
" longiseta
" pallide-fusca
" plicatilis
" sphacelata

Sorghum versicolor

Sporobolus fimbriatus
" [illegible]
" [illegible]
" panicoides
" pellucidus
" phyllotrichus
" pyramidalis
" spicatus
" stapfianus

Themeda triandra

Tragus berteronianus

L.M. Talbot
Serengeti-Mara [illegible] Research Project
c/o [illegible] Nairobi, Kenya, East Africa.
October 1959

*125 *126 check list proved a useful basis for grass plot work.

To determine successional changes and their time scales we placed much emphasis on the history of various forms of land use and of vegetation types. An outline of the history has been given above. The sources used included maps, early descriptions, records of governmental departments, and notes and diaries of local residents and others who had visited or worked in the area. In the north, particularly useful records were furnished by the Tsetse Survey and Control Division who had been carrying out research in the area since the 1930's.

General Description

*137 In the east are large open grassland areas, the Loita Plain in Kenya and the Serengeti Plain in Tanganyika. Toward the west the terrain is more wooded, all of it having been densely wooded in the past and now being in a fire-modified transitional state. There are riparian strips of forest along the major watercourses and patches of forest on the mountains, but the dominant woody vegetation is an open assemblage of low thorny trees, mostly species of *Acacia* and *Commiphora*. In appearance, many of the northern and western portions of the region that are not open grassland are a mosaic of open grass

4(27 areas divided by wooded watercourses, dotted here and there by bush thickets. Where fire has been excluded through overgrazing or protection, whistling thorn acacia (*Acacia drepanolobium*) quickly takes over much of the grassland, and in time may grow to 10 feet or more in height forming a dense but thin-stemmed forest through which more solid woodland trees may grow in time. The area between Seronera and the Kenya border, and that southeast of the central Serengeti Plain, is fairly close *Acacia* woodland, with thicker vegetation along the watercourses, and occasional open strips, meadows, or small plains.

Vegetation Types

Western Masailand lies within the humid-Hypsothermic zone as described by Heady (1960:12 et. seq.), this part of which has also been called the Scattered Tree Grassland (Acacia-Themeda) Zone (Edwards and Bogdan, 1951), and Open Grassland (Acacia-Themeda) Zone (Edwards, 1951), and the Tall Grass and Acacia-Tall Grass Savanna (Shantz and Marbut, 1923. For purposes of description I have recognized the following vegetation types (Fig. 4):

- Open Grassland
  - Tall Grass Plains
  - Short Grass Plains

(37

Bush

Woodland

Bushland

Thicket

Forest

Mountain Mist Forest

Cedar Forest

Riverine and Springhead Forest

These types will be described briefly below. About 115 species of grasses representing over 50 genera have been recorded from Western Masailand. In addition to these there are a vast number of forbs and shrubs. In one collection of the more common forbs from the southern part of the study area we had 86 species (122) representing 23 families. I shall not, therefore, give detailed lists of the species which compose the various vegetation types. Instead I shall describe the types listing only those species that are dominant or most obviously significant.

There are several very localized vegetation types which deserve a brief word but do not enter into the general discussion.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

¶ 137 There are two types of palm stands. The wild date palm (*Phoenix reclinata*) forms small dense clumps on several major rivers, including the Mara, Seronera, Mgungu, and Mbalageti. The Borassus palm (*Borassus aethiopum*) forms more open stands in grasslands and along rivers west of the Serengeti Plain. It stands up to 60 feet high, roughly twice the height of the date palm. Both palms appear quite fire resistant, and in places in Kenya and Tanganyika they appear to be the last survivors of wetter forests destroyed by fire.

The vegetation of the isolated kopjes in the open grasslands is sometimes considered as a separate vegetation type. The species involved are also found in woodland. When they occur on isolated kopjes we consider them to be relics of woodland, protected by the kopje formation, and they are considered below under the woodland types.

Tall Grass Plains.

This grassland type is found on the western Serengeti Plain (Fig. 32), south-western Mara Plains, and in smaller openings north and west of the Serengeti Plain. The grasses will grow to heights of from one to four feet and are dominated by *Themeda triandra*.

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Figure 50.

Tall grass plains in the west-central Serengeti Plains, near Lake Lgarya.

#(3) with a variety of other tall grasses important locally including species of *Bothriochloa*, *Chloris*, *Cymbopogon*, *Hyparrhenia*, *Setaria*, *Panicum*, *Pennisetum*. There is often a layer of medium-sized grasses including species of *Aristida*, *Digitaria*, *Eragrostis*, and *Sporobolus*. A ground level of small grasses including species of *Microchloa*, *Panicum*, and *Sporobolus* is usually present. A number of forbs are common but not normally obvious. Among the more common are species of *Euphorbia*, *Heliotropium*, *Justicia*, *Sida*, and various genera of Compositae and Cyperaceae.

#() These areas are burned frequently, usually annually and in a few places even more often. When low these areas provide food for a variety of wild ungulates. When the grasses are tall and dry wildebeests, zebras and the gazelles rarely enter them.

Short Grass Plains

The eastern plains of the Serengeti and the Loita are short grass areas. In the Loita Plain the tall grasses have been grazed out, and what remains are often short, less palatable grasses and forbs (Fig. 58). Grass dominants include species of *Aristida*, *Chloris*, *Cynodon*, *Digitaria*, *Eragrostis*, *Eustachys*, *Harpachne*, *Microchloa*, and *Pennisetum*. Forbs, including

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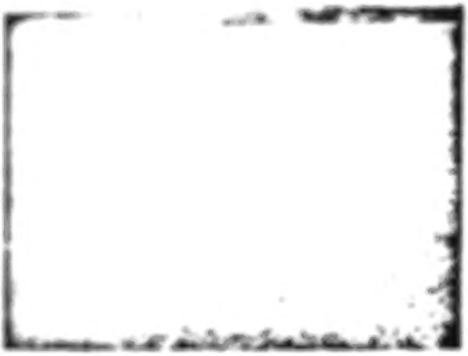

Figure 53.

Short grass plains in the eastern Mara. This area was formerly tall grass plain dominated by Themeda triandra but heavy grazing by domestic livestock has killed out the tall perennial grasses.

#137 species of *Becium*, *Justicia*, and *Sida* are very apparent.

In the short grass plains of the eastern Serengeti Plain heavy grazing is a factor, but there are apparently edaphic or climatic factors involved also in producing their short grass cover at least on the ash areas (Fig. 54). The species composition is much the same as the tall grass plains to the west but without the *Themeda*, and many of the other grasses appear dwarfed growing only a few inches high. There is a variety of conspicuous forbs, especially genera of Compositae, Cyperaceae, Convulaceae, and Euphorbiaceae. Most of this area does not burn because there is not enough fuel to carry a fire.

In a few spots farthest from water there is a good turf and the grasses appear less dwarfed. It would appear that with light grazing this country could develop a good grass cover which would to some degree protect itself from desiccation. With the very heavy grazing by livestock and game a turf cannot form on the loose soil. The scattered individual plants are subject to more desiccation than would a continuous grass cover, from factors such as wind and evaporation from the bare soil surrounding them and hence appear dwarfed. Soil

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Figure 54.

Short grass plains in the south-eastern Serengeti Plain. Here the soil is loose black ash. The grasses, including species of [illegible], Digitaria and Sporobolus, appear dwarfed and desiccated. Grass plants form small hummocks as the unprotected ash between plants is blown away.

19h Talbot K-4,5 (1956-1962)1964 FL.12 Masai FL.12

8 [3] moisture could be found less than a foot under the surface under the few areas with a fair grass cover for several days following the scattered dry season rains, while the adjacent bare areas were dry for several feet down within an hour after the rain stopped.

In the southern Serengeti Plain the grass is short but it is apparently so because of heavy grazing. There are many annual herbs, two species of the white flowered *Leucas*, spiney *Crotalaria spinosa* and *Indigofera basiflora*, and a number of annual grasses, all indicating overgrazing.

Woodland

I am using *woodland* in a very broad sense to refer to areas with a grass cover and trees of about 20 feet or more in height (Fig. 55, 56, 57). The trees vary from relatively scattered individuals, which would be termed *open woodland*, to *closed woodland* where there is a closed or almost closed canopy but where there is still grassland beneath. The dominant genera of woody vegetation is *Acacia*, with fifteen species, *Albizia* with two, *Commiphora* with five, *Ficus* with about seven, *Cordia* with three, *Grewia* with five, *Lannea* with four, *Ziziphus* with two.

Figure 33.

Giraffe in open woodland. The dominant trees are species of *Acacia* and *Commiphora*. The grass cover is identical with that of open tall grass plains nearby, dominated here by *Themeda triandra*.

Figure 58.

Seronera Camp, headquarters of the Serengeti National Park. This grove is typical open Umbrella Tree woodland. The trees are *Acacia tortilis spirocarpa* and *A. [illegible]*. Dominant grasses are *Themeda triandra*, *Cynodon dactylon* and *Sporobolus* spp. This picture was taken in 1956. Since 1956 a number of barracks-like office buildings and tourist accommodations have been built, and the camp has lost its primitive character.

#13

Figure 57.

Acacia woodland west of the Serengeti Plain. Fires are irregular enough here that there is some reproduction of the acacias. Where grazing is relatively light and fires are regular there can be virtually no reproduction. The dominant grass being fed on by the zebras is Themeda triandra.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

4 137

Woodland is found west, southwest, and north of the Serengeti Plain. There are also patches within the Serengeti Plain at various places. Woodland is discontinuous having within it areas of open plains (Fig. 50), bushland, and forest.

The grasses under this woodland are in general the same as those in open tall grass plains. Locally there are other dominants such as various species of *Hyparrhenia*, *Cymbopogon*, and *Panicum*.

The typical mature open Umbrella Tree Woodland is seen at Seronera Camp (Fig.56). The trees are mostly Umbrella Acacia (*Acacia tortilis spirocarpa*) and Stick Bark Acacia (*Acacia clavigera*). Dominant grasses are *Themeda triandra*, *Cynodon dactylon* and species of *Pennisetum*.

There are several groves of Fever Tree Woodland in the study area. These are dominated by the yellow barked Fever Tree (*Acacia xanthophloea*), ranging from 40 to about 60 feet high. These groves appear to be located where ground water is relatively stable and high. Usually they are in valley bottoms or beside lakes, and small groves are found from the Guaso Nyiro River

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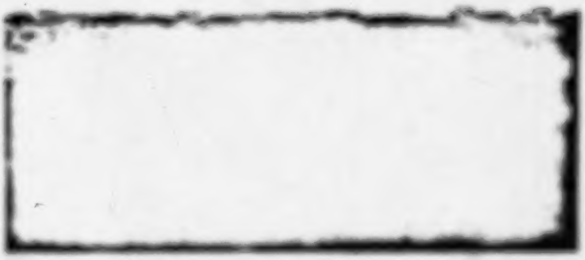

Figure 58.

Area of open grass plains in a closed Acacia-Commiphora woodland. The topi is standing in Pennisetum mezianum.

137 and Lemek Valley in the north throughout Western Masailand to the southern Serengeti Plain and the Ngorongoro Crater. Thicker stands (Fig. 59) have a closed canopy in places and a shrubby understory composed of shrubs such as *Cassia didymobotrya*, *Capparis tomentosa* and *Lycium merkeri*. Grasses include shade tolerant species of *Chloris*, *Sporobolus*, *Eriochloa*, and *Setaria*. More open groves or remnants of groves (Fig. 60) are frequent, usually in tall grass plains areas.

Bushland

Bushland is essentially grassland with more or less dense woody vegetation under about 20 feet in height. It ranges from an open stand of Whistling Thorn (*Acacia drepanolobium*) (Fig. 35), through a kind of orchard steppe (Fig. 61) and the density of woody vegetation varies greatly. The dominant woody species are various species of *Acacia* (particularly *A. drepanolobium* and *A. seyal*) and *Commiphora*. The grasses are the same as those in adjacent grasslands.

Thickets

Thickets or bush islands are found throughout the study area, particularly around most hills, where the formation may become a wide belt rather than an

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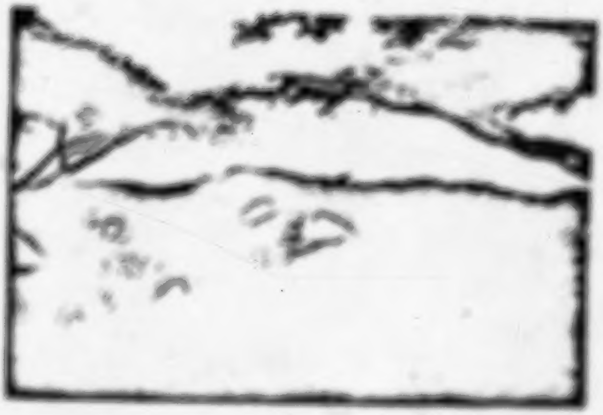

Figure 68.

Cover from woodland, near the edge of a closed stand of *Acacia xanthophloea* with an understory of shade tolerant shrubs and grasses.

Figure 60.

Wild dogs in an open Fever Tree Woodland. Here there are a few Umbrella Acacias as well as Fever Trees.

#13

Figure 61.

Orchard Steppe Bushland, with *Combretum* spp. in *Themeda* grassland otherwise identical with the open plains beyond. Three male lions with a zebra kill.

#137 island, and on ridge tops in rolling grasslands.

The formation is typically a dense thicket 10 to 15 feet high with occasional taller trees standing above it, frequently dissected by damp game trails. The taller vegetation may include the Euphorbia candelabrum, Albizia schimperiana, Salvadora persica, Balanites aegyptiaca, and Acokanthera schimperi. The body of the thicket may include several Acacias, particularly A. mellifera and A. brevispicata, various species of Aloe, Commiphora, Grewia, Cissus, Croton, Boscia, and many others. Sansevieria robusta is often a peripheral plant in these thickets.

#136 #137 These thickets provide cover for a variety of wild animals. Buffalo, rhinoceros and giraffe are common inhabitants. In grasslands they are so frequently used by lions as a retreat that Darling (1960) termed them Lion Bush.

#137 Mountain Mist Forest

This type is not strictly in Western Masailand, but it adjoins it on the south on the higher parts of the Ngorongoro Highlands (Fig. 43). Originally this forest must have extended far below its present level,

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Figure 65.

Mountain rain forest on Mt. Oldeani, Ngorongoro Highlands.

127 but continued burning by the Masai and their predecessors has greatly reduced its extent. There are numerous little protected islands of this forest in the surrounding lower grasslands, and there has been some retreat of the forest due to burning in the six years between my first and last visits. Abundant trees in the undisturbed areas are _Bersama abyssinica_, _Cassipourea malosana_, _[illegible] [illegible]_, _Ekebergia rueppeliana_, and _Teclea simplicifolia_. There is a dense undergrowth and numerous vines and epiphytes.

Cedar Forest

In a few drier or better drained areas of the Ngorongoro Highlands there are stands of cedar (_Juniperus procera_), with some _Bersama abyssinica_, _Olea chrysophylla_, and _Cassipourea malosana_. _Podocarpus milanjianus_ is also found in these montane forests. The cedar association has been almost completely destroyed by burning, and the last remnants are on steep slopes in two craters and in narrow ravines.

The Mau Forest on the Mau Escarpment is dominated by cedar, podo (_Podocarpus milanjianus_), and olives (_Olea_ spp.). There are two types of cedar forest on the Mau, a moist forest to the west and a dry one to the east. Although the dry forest has a slightly lower

*(3) rainfall than the moist forest, when the moist forest is cleared the regrowth appears identical with the dry forest formation of the same altitude. In the dry forest there are islands of moist forest protected by topography from fire and grazing. In the moist forest the dominant trees are cedar, podo and olives, with a profusion of other less common trees. Woody undergrowth includes species of Croton, Rhus, Grewia, Euclea, and Tarchonanthus. In the dry forest cedar is often in pure stands and the undergrowth is dominated by leleshwa (Tarchonanthus camphoratus), Grewia and Rhus.

Cedar forest is also found on the Loita Plateau, where it is fast retreating due to fire, and in small patches on higher hill tops throughout the region.

Riverine and Groundwater Forest

Along the more permanent watercourses and around the larger springs there is a dense evergreen forest. In places where the canopy is more open and around the edges of the forest there is a thick brushy undergrowth (Fig. 43). In the larger patches of forest the tall canopy shuts out the sun and there is little undergrowth. The best examples remaining of this type are along the Mara River. Everywhere else the forest has retreated

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#13

Figure 63.

Black rhinoceros in bushy undergrowth characteristic of the edges of riverine forest.

19: Talbot E-4,5 (1956-1962)1964 Fl.12 Masai Fl.12

to the edge of the watercourses where it remains as a thin strip of trees rather than a block of true forest.

The trees involved include species of _Ficus_, _Warburgia_, _Podocarpus_, _Diospyros_, _Chaetachme_, _Euclea_, _Allophylus_, _Kigelia_, and numerous others. Some olives and numerous acacias are found around the forest edges. Underbrush includes most of the components of the thickets, discussed above. Grasses where present include large, coarse species of _Brachiaria_, _Hyparrhenia_, _Panicum_, _Setaria_, and _Sporobolus_.

GRAZING

(37 Domestic Livestock

22(Domestic livestock show clear preferences for
21) certain grasses in the study area (Heady, 1960; Talbot, 1960; and above). The preferences of cattle, sheep, goats, and donkeys largely overlap. Although goats are reported to be browsers, in the study area they graze with the sheep and their preferences appear the same. When preferred grasses are not available livestock will resort to whatever plants are left, but before resorting to second choice foods they will seek out and eat
(37 most of the first choice ones. If grazing pressure is too great the preferred grasses will be eaten out and will remain only as occasional relic plants protected from grazing by thorn bushes and rocks. Heavier grazing pressure will remove second choice foods leaving only the least palatable plants and those protected by spines or similar growth.
(16] Different species of wild ungulates have clear preferences in food plants also, as described above. Thus, by analysis of the grass composition of an area, it should be possible to determine its recent grazing history.
(37 Part of Dr. Heady's grassland research in East Africa
(26 involved this type of determination, and a summary of

*157 *156 the gross effects of grazing on species composition in different grassland types is given in his publication on Range Management in East Africa (Heady, 1960). He generously described his methods and findings to us and we have used his work as a basis for our analyses of the impact of grazing.

*158 Different species of grass can stand heavier grazing than others. According to Heady (1960:41, et. seq.) the perennial bunch grasses can stand removal of 50 to 60 per cent of their annual growth. Grasses with rhizomes (such as Cynodon) can stand more.

F:57 *3.12 Under Masai grazing management virtually any grazing in the study area is overgrazing. This fact is due to several factors, chief among them being too many animals, herds too tightly packed, and areas being grazed too early and too long.

*157 Under heavy livestock grazing the first effect is to diminish and kill out the palatable bunch grasses. Themeda is the most sensitive single species and best indicator grass. In areas unpressured by domestic livestock Themeda triandra makes up from about 40 to 80 per cent of the grass cover (by species composition). This per cent drops rapidly with livestock use, and is heavily

127 used areas it may be present only as a trace. Other grasses preferred by livestock decrease in a similar manner. A significant reduction in these species can be noted after two to three years' grazing.

In areas long grazed the larger perennial bunch grasses are almost totally removed by grazing and trampling. A few small perennial grasses remain, such as *Microchloa kunthii*, *Sporobolus festivus*, and *Harpachne schimperi*, various species of *Aristida*, *Eragrostis*, *Panicum* and other annuals are present. *Pennisetum mezianum*, almost uneaten by livestock, becomes dominant on overgrazed areas of clay soil. and often on other types. Further grazing and trampling will destroy most of the above grasses, leaving weeds and woody shrubs -- which were present in small numbers in the former grassland -- dominant. *Aster*, *Crotalaria*, *Dyschoriste*, *Indigofera*, *Justicia*, *Leucas*, *Sida*, and *Solanum* become dominants on extremely overgrazed land.

In tall grassland ungrazed by livestock there are often over 20 species of grass that are common and a number of other less common ones. In areas overgrazed for only about five years there may be only five to ten that will show up on a 300 to 400 point transect.

*137 The basal cover, or amount of ground surface covered by the bases of live plants, ranges from about 50 to 80 per cent under tall grass plains ungrazed by livestock, to about five per cent where grazing by domestic livestock has been heavy for six or seven years. Part of this effect is due to the replacement of the bunch grasses whose bases cover a relatively large area per plant, by weeds, annuals and perennials whose bases are often single stalks, and by seedlings of perennials. With lower basal cover more of the surface is exposed to erosion and the remnant plants are left on pedestals or hummocks.

Overgrazing normally allows invasion of woody plants by removing competition from bunch grasses and by excluding hot fires.

Wild Ungulates

*136
*137 Mixed species of wild ungulates in the study area normally utilize virtually all plants in the grassland because of the diets discussed above. The animals are constantly moving and the grazing pressure is widely spread. Starting 24 to 36 hours after a good rain many perennial grasses will grow about an inch a day, often for about a week. By that time the grass is too tall and rank for wildebeests and Thomson's gazelles, for

*137
[134] example, and they move on. Some years the grazing pattern may leave little dry grass standing in a given area and a hot fire will not be carried there. But other seasons' pattern will be different and the remaining dry material will carry a hot fire. Even in areas where the yearlong biomass of wild ungulates is highest there is usually enough dry grass left standing at some season each year to support a fire.

Where the grass cover is not utilized by grazing, burning, or clipping, the larger bunch grasses grow into very large clumps, dead at the center, with bare ground between them. The ground cover in such areas may be from around 40 to 55 per cent. Small grasses disappear presumably through competition with the larger ones, and typically only 10 to 15 species will be common. The effect of grazing, clipping, or some fires is to maintain a grass cover composed of many vigorous medium sized bunches, rather than a few large bunches in undergrazed land, or many seedlings or annuals in overgrazed land.

*13 Figures 64 through 72 illustrate the effects of different degrees of grazing, with consequent changes in vegetation composition and soil cover.

#13

Figure 64.

Themeda grassland after moderately heavy grazing by about 20 species of wild ungulates. Roughly 30 species of grasses are present and total cover is over 60 per cent. Fires are annual.

19: Talbot K-4,5 (1954-1962)1966 PL.12 Mosaic PL.12

Figure 65.

Originally Themeda grassland, heavily grazed by domestic livestock for about five years. Most Themeda is gone and the dominant grass is Pennisetum mezianum, ungrazed by domestic livestock. Although the crown cover here appears good, the basal cover is only around five per cent. There are about five common species of grass here.

19: Talbot K-4,5 (1954-1962)1964 PL.12 Masai PL.12

*13

Figure 88.

Slightly undergrazed Themeda grassland. The grass clumps are large with bare spaces between. Ground cover is around 50 per cent and there are about 15 common species of grass. Fires are hot and keep out brush. The area has just been grazed fairly heavily but in most previous seasons grazing has been very light.

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Figure 67.

hemeda grassland grazed seasonally by cattle for one
ear and sheep and goats for about four years. The
pecies composition has been changed, basal cover
educed, and since fires have been excluded by heavy
razing, shrubs are invading.

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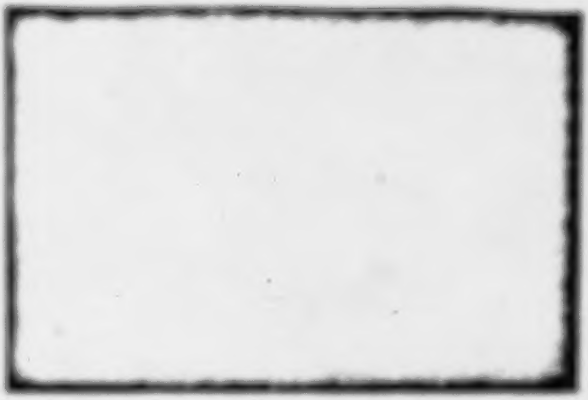

Figure 68.

Effect of animal trails in the loose soil areas of the eastern plains.

19: Talbot K-4,5 (1954-1962)1964 Pl.12 Masai Pl.12

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Figure 69.

Overgrazed grassland invaded by shrubs and coarse grasses.

#13

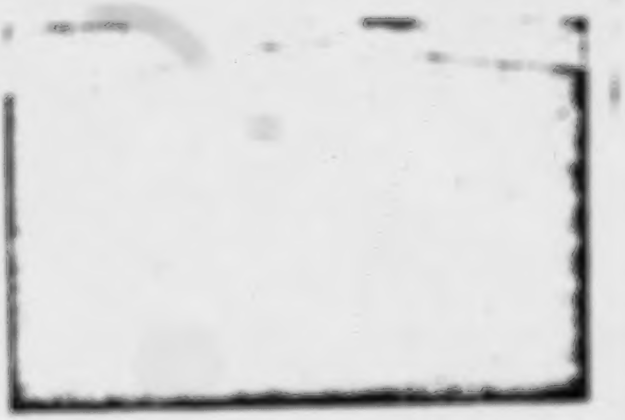

Figure 78.

Shrub invasion on overgrazed tall grassland in a high rainfall area of the southern Serengeti.

19: Talbot E-4,3 (1954-1962)1964 Pl.12 Masai Pl.12

Figure 71.

Shrub invasion in badly overgrazed former Themeda grassland on Loita Plain. Shrubs are largely *Euphorbia* and *Sida*, and perennial grass has almost disappeared completely.

Figure 72.

Eastern Serengeti Plain. Limestone visible where overgrazing has removed the grass cover and wind erosion has removed the loose volcanic ash soil.

19: Talbot K-4,5 ((1956-1962)1964 FL12 Masai FL12

F 13? Trampling

Trampling can be a factor in killing some perennial bunch grasses, while annuals and perennials such as *Pennisetum* are quite resistant to it.

134 Where domestic livestock are herded back and forth along the same routes the hooves cut through the turf and cause some erosion (Fig. 68). In areas of loose soil, especially in the eastern plains of the study area, this factor is quite serious.

F 13 Wild animals also create trails. During the seasonal migrations long lines of zebras and wildebeests follow one another nose to tail and the resultant trails are quite conspicuous (Fig. 72). Since these trails normally are only used once each season the erosion effect is minimized. Where migratory movements are compressed into saddles between hills or narrow valleys these trails are worn very deep and have become a characteristic physical feature of the country.

F [233] Domestic livestock are closely herded in tight bunches (Fig. 24 and 25) which accentuates trampling damage. The wild animals graze in open formation. Even large herds of wildebeests are relatively openly spaced (Fig. 74) which reduces trampling damage, even from very large numbers of animals.

19: Talbot K-4,5 (1954-1962)1964 Pl.12 Masai Pl.12

#13

Figure 78.

Trails made by migrating wildebeests and zebras. The animals often move through this plainsland during the dry season movements. Old trails can be seen paralleling the fresh ones. Trails used in the season when the photograph was taken (1961) are clearly recognizable by the dark appearing fresh dust in the trails and downwind of them (away from the camera). Zebras are in the nearby trails and large herds of wildebeests are near the far tree line.

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[233]

Figure 78.

Herd of wildebeeste grazing. Even large herds, while grazing, move in an open formation which reduces trampling effect relative to domestic livestock which are herded into tightly packed bunches.

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FL.

FIRE

Burning as the lack of it can determine the vegetation patterns within the study area. But fire is dependent upon fuel left as removed by the grazing animals, and on the season and timing of the burn which is determined by the Masai, Africans outside Masailand, and Europeans (and now National Parks officials) who light the fires.

Except for the short grass plains of parts of the eastern Serengeti and Loita Plains, virtually the entire area of Western Masailand was burned at least annually during the period of study. There are numerous small islands which the fires miss, and a few fairly large areas which are protected for various reasons, but fire is very general.

137 Throughout most of the open grasslands there are shrubs and woody growth. These are suppressed by frequent burns. In areas burned annually the woody vegetation may appear as "seedlings" following the rain, yet examination of the "seedlings" shows that they have an extensive root system culminating in a hard often-knobby crown at ground level. They are several years old and apparently enough energy can be stored

137 from the year's net current growth to maintain the root system for the rest of the year if necessary. The annual fires kill back the year's shoots. Therefore in appearance these are pure grasslands with no woody growth. However, given a good wet season and no subsequent fire the woody vegetation grows vigorously and grassland can be transformed to light bushland in as little as two seasons. Whistling thorn (Acacia drepanolobium) is a particularly good example.

In open grasslands we have found root crowns of Whistling Thorn over three inches in diameter, with several foot long root systems. Without burning, these plants can grow at least 18 inches a year for several years (Fig. 25), and we have measured over two feet of growth during the first season. After three or four years only the hottest fire can kill them. Where grazing is moderately heavy the fires are too light to kill the thorn and only kill the lower lateral branches. The Acacia then puts on growth at the top, and in eight to ten years on good sites whistling thorn can form an open or closed woodland of slender-straight 15 foot high trees with virtually smooth lower trunks.

A stand of Whistling Thorn five years old or

*(37) sides can be suppressed only by an extremely hot fire, usually resulting from several seasons' accumulation of dry grass. Under such conditions, if the fire occurs near the end of the dry season (August to October) the woody growth can be suppressed and part of it killed (Fig. 75). Such effective fires are not likely at present, however. The grazing pressure is heavy wherever domestic livestock are grazed, and fires are started whenever the grass will burn, usually early in the dry season when they have the least effect on the brush, even in country where some accumulation of grass is possible. Consequently during the past ten years there has been a steady encroachment of Whistling Thorn into Masai grazing lands (Fig. 76).

Several other species of _Acacia_, including _A. hockii_ and _A. seyal_ have a similar reaction to fire. The distribution of these Acacias is not uniform apparently due to a combination of soil conditions and moisture. It is widely believed in East Africa that the distribution of Whistling Thorn is determined by soil, that it grows on heavy clays with impeded drainage. The most vigorous growths of Whistling Thorn that we have noted have been in clay areas with moderate to good drainage. This observation is supported by Birch (1952)

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Figure 7b.

A stand of roughly ten foot high *Acacia drepanolobium* killed by an extremely hot grass fire late in the dry season.

*13

Figure 76.

Formerly open grassland, unburned or lightly burned for a series of years because of overgrazing by domestic livestock, being invaded by Acacia drepanolobium. The open area in the mid background is a poorly drained bottom. The exclusion of Acacias from that area may be due to impede drainage or to hotter fires carried by the lightly grazed coarse grass of the bottom.

*137 who found in black cotton clay near Nairobi that the higher the water level the fewer the Whistling Thorn plants. In Figure 76, the one area not invaded by Acacia is a poorly drained bottom in the mid background. This could be due to the drainage, or to the coarse high grass there which supports a hotter fire than the better drained and more heavily grazed lands around it. As described above muddy bottoms are often avoided by wild ungulates. The distribution of mud during the growing season of the plants often determines the distribution of that season's grazing by the animals, and, therefore, the distribution of standing grass and of hot fires.

Whistling Thorn also can be found on virtually every other soil type in the area. One factor affecting its distribution may be the length of time an area has been regularly burned grassland. We have observed seedling Whistling Thorn bushes invading areas where there were no well-rooted but suppressed plants. The Acacia obviously could grow there and the apparent limiting factor was distribution of seeds. In areas long under grassland the viable Acacia seeds may have been germinated and killed by fires and the Acacia *[126] plants killed. Giraffes and rhinos are the primary animals that feed on Whistling Thorn and that would be

*127 expected to spread the seeds through their faeces.
*136 Neither animal normally penetrates far into open grasslands.
Other animals might eat the seed pods, though we have
*137 no record of them doing so. Consequently distribution
of the seeds may be a limiting factor in the return
of the Acacia into areas from which it has been
exterminated.

The most dramatic impact of fire is on the
existing forests and thickets. Each season that a hot
fire burns up to a patch of moist forest it kills an
outer layer of branches, trees and brush. These
dry and provide tinder for a hot fire the next season,
which in turn kills more of the forest growth, gradually
pushing the grassland into the forests (Fig. 77 & 78).
*[136] Elephants accelerate the process by pushing down trees
and pulling down large limbs, providing more fuel and
opening fire routes into the denser vegetation. Their
effect is conspicuous in the Mara with its high elephant
population. The result is open grassland with trees
limited to watercourses where moister conditions and
sometimes topography protect them (Fig. 79a). With
long continued burning the eventual result can be open
grassland completely devoid of trees. Even when fires
cannot kill the last large trees, they can kill

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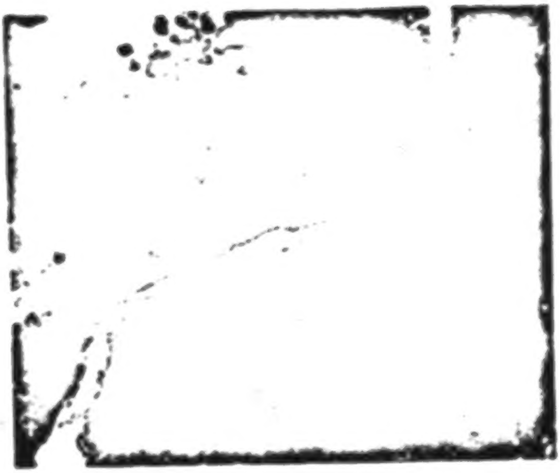

Figure 77.

Fire burned into riverine forest. An outer layer of branches, shrubs and trees has been killed by the fire, and these will provide hot fuel for further penetration of the forest by the next fire. Note the animal tracks leading to the watering point across the river.

F13

Figure 78.

A burn stopped by riverine forest. The prevailing wind is from the left, and the bend in the river has protected the remnant of forest on the down wind side, while the fire is blown into the forest on the upwind side.

*13

Figure 79a.

Mara Plains in Kenya. Fires have cleared the woody vegetation from the flats, leaving remnant strips of forest along the rivers and in the gullies. This area is not grazed by domestic livestock and it is one of the most biologically productive grasslands in Western Masailand.

*137

reproduction and the relic trees will stand alone in an open plain until they die of old age (Fig. 79b).

*13

Slight changes in relief can stop fires. A stream bed with a significant bank or wide expanse can stop most grass fires even where no riverine strip exists (Fig. 80). A bend in a river can protect the vegetation inside the bend if the prevailing dry season winds do not blow directly into the bend (Fig. 78 & 81).

Forest or thicket often survive on hill or ridge tops longer than in the bottoms or flats. During wet periods the ungulates congregate on these higher, better drained areas. Their grazing is often much heavier there than in lower areas, and hence there is less standing vegetation in the dry season, the fires are light, and any woody vegetation is somewhat protected (Fig. 82 & 83).

Ant/(termite)hills are found throughout the wooded areas. In most of the study area large live ant hills are not found in open grassland. Dead ant hills are frequent in open grassland and they are gradually worn down, often by zebras, wildebeests, topis, and other ungulates using them as rubbing or rolling grounds. The ant hills are most evident where forest or closed

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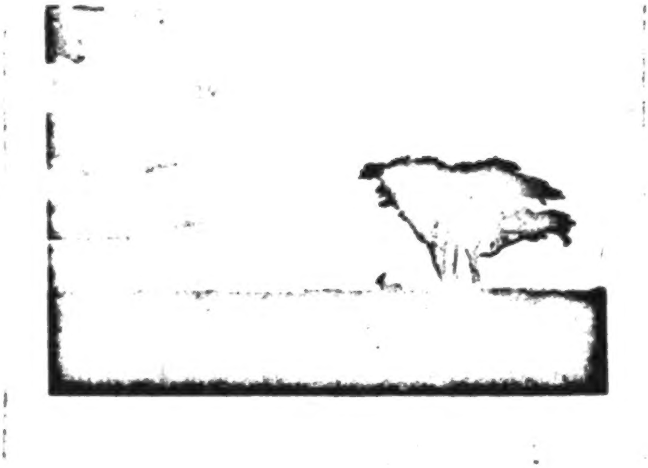

Figure 79b.

Two relic Acacias on the Serengeti Plain. This area was formerly an Acacia parkland. Fires kept it open and prevented reproduction of the Acacias, most of which have died.

#13

Figure 80.

Fire stopped by a minor physical barrier, a dry sand river. The many game tracks are converging on a salt lick.

f13

Figure 81.

Relic forest protected from fire by bends of the dry river.

*13

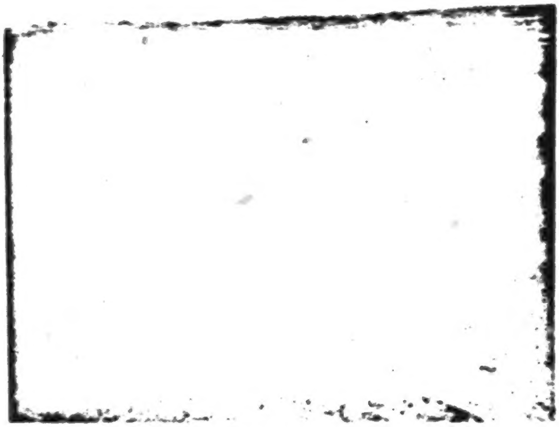

Figure 82.

Mara Plains in Kenya. Remnant patch of forest on a low hill. Heavy grazing on the well drained hill thins the grass and partically protects the forest from fire. Heavier grazing and trampling (which shows as a lighter zone in the dark grass) around the forest patch provides a further fire break effect.

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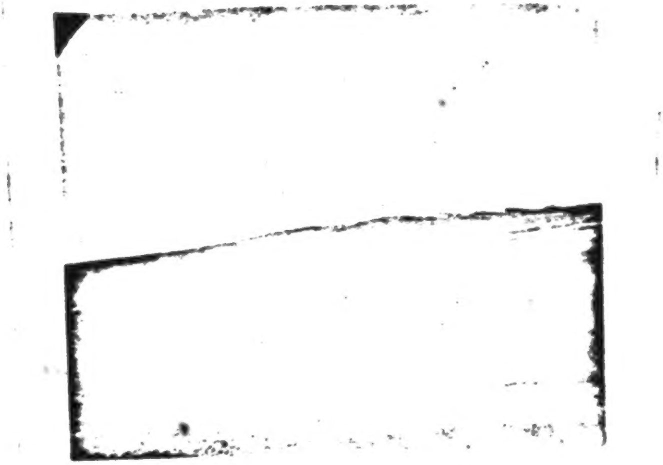

Figure 83.

Remnant patch of forest on a low hill top. The forest is partially protected from fire by thinner grass caused by heavier grazing on the well drained hill especially at the edge of the forest which shows light against the darker tall grasses.

*13 woodland has very recently been cleared or is in process of being cleared by fire (Fig. 84). Remnant ant hills can also be seen from an airplane scattered through flatter areas that are presently grassland (Fig. 85). We regard the existence of these dead ant hills throughout the grassland areas as further evidence that they were formerly wooded. The ant hills usually occur on better drained areas, usually on slight slopes. They form a characteristic pattern on slopes (Fig. 84) also noted by Darling (1960:17). Similar patterns are found over much of the Loita Plain and parts of the Serengeti. The interesting slope pattern appears caused by vegetation, grazing and drainage. The ant hills are slightly better drained and higher than the surrounding slope. Slope drainage goes around them. The species composition is slightly different between the ant hills and the swales, the hills having Cynodon, usually heavily grazed, and other plants of early successional stages, while the swales have tall grass species. Also the ant hills frequently support a woody vegetation for a time after it has been burned away from around them.

*137 Some grasses seem to be favored by periodic burning. Themeda is one such, and in areas little burned it becomes a less important part of the grass

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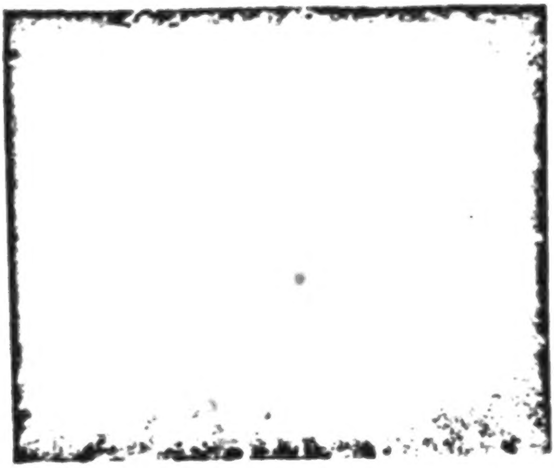

Figure 84.

Pattern of ant hills (termite mounds) on hillside recently cleared of trees by fire. Remnant patches of former vegetation remain on some ant hills, protected by the fire break effect of the ant hill sides.

*13

Figure 85.

Pattern of flattened ant hills in flat open grass plain.

* 137 cover. Themeda is very fire resistant and presumably frequent fire weakens its competitors. Themeda is most abundant in grasslands where there have been particularly hot fires late in the dry season. Lighter fires appear to favor a more varied species composition.

Following a burn in moist conditions many grasses sprout immediately. They put on more growth for several days than the same species outside the burn, then the growth rate slows and those outside the burn catch up. Grasses in a burn are much more heavily grazed than those in adjacent unburned areas. The present pattern of burning, up to four times a year where there is enough grass to burn, appears to be defeating the purpose of the burners. There is not time allowed for accumulation of fuel and the fires are light. Shrubs, weeds, and woody growth are therefore invading the most heavily burned areas. In areas with two or more burns in a year the subsequent grass growth appears less vigorous than in less frequently burned areas. _Themeda triandra_, for example, may grow less than one foot tall the year following two to four burns, while in an adjacent similar site where it was only burned once it may reach three to four feet.

*13

VEGETATION SUCCESSION

If a piece of bare ground is protected from disturbances such as fire and grazing various forms of vegetation will colonize the area and then succeed one another, each form altering the conditions somewhat and in effect, making living conditions possible for its successor and less suitable for its predecessor. The vegetation of Western Masailand is a mosaic of the vegetation types outlined above. Yet there appears to be one basic succession that obtains, with local variations, over the entire area. Extremes in factors such as subsurface moisture, soil Ph., soil depth, and exposure will cause variations in the species composition of the successional stages, but the general pattern appears quite uniform over the study area.

A description of undisturbed successional stages is quite artificial for two basic reasons: First, disturbance is almost always present in the form of grazing animals and fires. Second, even if undisturbed, a succession is a gradient of changing conditions rather than a series of separate stages; a slope rather *137 than a stairway. Therefore the "stages" outlined below are intended to show trend and the species and forms

*137

listed are intended to illustrate the characteristics of the gradient at that point but not to describe a discrete vegetation type. These are in outline form; they are not intended to be exhaustive or exclusive descriptions.

1. Bare ground.

2. Colonization stage: various small succulents including several species of *Portulaca*; a ground *Euphorbia*; several species of *Cyperus* and *Kyllinga*; Stoloniferous grasses including *Cynodon* and *Digitaria*; a few annual grasses including small forms of *Aristida* and *Panicum*, and small perennials including *Microchloa* and *Harpachne*.

3. A variety of grasses, forbs, shrubs and low woody plants. In the grasses are some annuals but there is a preponderance of perennials. Grasses include species of *Andropogon*, *Aristida*, *Bothriochloa*, *Cenchrus*, *Chloris*, *Cynodon*, *Digitaria*, *Eragrostis*, *Eustachys*, *Microchloa*, *Panicum*, *Pennisetum*, *Sporobolus*, and *Themeda*. Forbs include sedges and sedge-like plants, composites, *Sida* and *Justicia*. Woody plants are dominated by low Acacias, especially *A*. *drpanolobium* with leleshwa above about 6,000 feet.

4. This stage includes many of the above grasses and forbs, but the woody vegetation is taller and thicker. Taller vegetation includes forms of Acacia

#137

(tree form of *A. drepanolobium*, *A. brevispica*, *A. mellifera*, and occasional others), *Aloe*, *Acokathera*, *Balanites*, *Boscia*, *Cissus*, *Commiphora*, *Cordia*, *Croton*, *Euphorbia*, *Grewia*, *Leleshwa*, and *Olea*. In form this stage is an uneven, three level woodland. The taller trees stand above a fairly thick but discontinuous undergrowth mixed with grasses and grassy open spots.

5. A more uniform closed forest with a canopy ranging from 30 to 60 feet, and tree, shrub, and herb layers down to ground level. The grasses are shade tolerant forms, particularly species of *Digitaria*, *Enteropogon*, *Panicum*, *Setaria*, *Sporobolis*, with *Cenchrus*, *Eriochloa*, *Pennisetum*, and *Setaria*, and a few of the above grasses in the more open areas. The trees include some tall Acacias (especially *A. kirkii*, *A. polyacantha*, and *A. xanthophloea*), *Albizia*, *Cassine*, *Cordia*, *Diospyros*, *Euclea*, *Ficus*, *Garcinia*, *Podocarpus*, *Kigelia*, and above about 6,000 feet, cedar.

Lower levels include some of the species from stage four above, plus *Gardenia*, *Allophylus*, *Cordia*, *Croton*, *Erythroxylum*, *Meeboutonia*, *Ziziphus*, and numerous others. Grasses are entirely shade tolerant species, mostly tall and coarse.

6. The final stage of which there is any evidence in the study area is a closed-canopy, multi-layer,

#137 broad leaf forest in the lower areas grading into a moist cedar-podo-olive forest on the slopes around 6,000 to 7,000 feet elevation, and that grading into a mist forest at its upper edge.

#13 Environmental conditions in some areas will alter the above structure. Examples are the eastern Serengeti, with its periodic deposits of ash, and the moister areas below 4,000 feet near Lake Victoria.

The earlier stages above succeed each other relatively rapidly. To proceed from stage four to stage five may require 50 years or more. From stage five to six may require centuries.

The speed with which this succession proceeds depends upon the moisture. In areas with less rainfall the vegetation cover itself gradually increases the humidity at ground level and under the vegetation canopy. For example, where sufficient moisture is present in the ground to support stage three, stage two is passed very quickly. However, in areas with low initial ground water and relatively low rainfall the vegetation cover itself gradually increases the humidity at ground level and the ground water. Under such conditions

*13 passage from stage two to stage three might take very much longer. As noted above, there are areas where because of various factors, edaphic or otherwise, the succession outlined above will not occur.

*137 There does not appear to be any pure grassland stage in the "climatic" succession in Western Masailand. Where they appear grasses are a part of a more varied vegetation.

*13 IMPACT OF FIRE AND GRAZING ON SUCCESSION

The impact of fire and grazing on vegetation succession in Western Masailand depends on their intensity and at what point in that succession they exert their influence. Depending on their occurrence and intensity fire and grazing can create and maintain woodland or bushland of varying densities , thickets, open grasslands, or semi-deserts.

Very hot fires can create open, treeless grassland out of virtually any assemblage of woody vegetation. During the period of study fires were seasonally creating open tall grasslands at the expense of the thick riverine forests along the Mara and Bologonja Rivers. The more humid the forest the longer its reduction by fire will take. In Western Masailand, as noted above, there are frequent short dry periods but also occasional long droughts. The greatest incursions of fire into vegetation occur during these irregular periods. The period of several dry years culminating in 1961 was one such severe drought, the driest in the memory of residents. During 1961 the Masai told us that they had been able to burn areas that they had never before burned in their memory. The impact of grazing was

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especially pronounced also at that time. It is clear that fire and grazing exert their greatest impact during these occasional prolonged droughts when the vegetation is most vulnerable to desiccation.

In the discussion below, I shall describe the effect of fire and grazing on vegetation succession essentially in outline form.

Tall Grass and Short Grass Plains

The tall grass plains of Western Masailand are an extremely complex formation or successional stage created and maintained by grazing and burning. They are not a community that occurs in the normal plant succession of the area. Fire will create open grassland from any more woody stage, and as described above, fire and grazing will maintain it in the form of a vigorous Themeda grassland with many species and a high ground cover.

Overgrazing leads to short grass plains, to shrub- and weed-lands, and eventually to semi-desert conditions where rainfall is very low. Where it is higher the short grass stage leads to shrub and woody brush invasion (Fig. 76).[1]

[1] [See p. 370.--Analyst]

*137

Bushland

Removal of fire without overgrazing from a Themeda grassland normally leads to brush invasion. Whistling Thorn and other Acacias grow up through the grassland, eventually forming a thin-trunked bushland standing 15 to 20 feet high. Commiphora and other low trees of successional stage four(described above)may be scattered through this light Acacia bush. The grasses remain much the same as in the tall grass plains if they are grazed. If not grazed, with the protection from fire needed for this succession, the grasses follow the undergrazing changes described above.

If fires are again introduced at this point and they are hot and regular, they can result in re-establishment of the open grassland. If, as is more common, they are irregular and not too hot, they maintain a thin low Acacia bush or woodland.

If fires are not introduced at the thin Acacia bushland stage, other vegetation of the normal successional stage four (described above) appear to grow up through the original Acacias and in time replaces them.

*137 Woodland

If succession is inturrupted again by fires at about stage four an open or closed Acacia woodland will result. Periodic fires will maintain this form. The variety and vigor of grass species depends largely on the grazing. Frequent hot fires remove undergrowth and prevent tree reproduction, creating open parkland (Fig. 56). If the fire pattern is continued, reproduction of the trees is prevented and the area becomes open grassland on the death of the existing trees (Fig. 79b). If the fire pattern is intermittant, possibly due to periodically heavy grazing, some reproduction may take place and the park woodland can be relatively stable (Fig. 57).

The type of woodland that results from periodic fires in successional stage four appears to depend largely on the available moisture and the temperature of the fires. This vegetation type does not maintain moist conditions as a closed broad-leaf forest does, therefore, it is more vulnerable to desiccation. With light grazing, considerable accumulation of dry grasses, and hot, late dry season fires, the result is an open woodland or orchard steppe. With irregular fires and at least periodic moderate to heavy grazing a closed or semi-closed scrub woodland develops. Rocky,

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

*137 dissected terrain favors such a formation because of the discontinuous fire patterns it produces. The species composition and vigor of grasses under this stage, as those under any woodland or open grassland, depend on the pattern of grazing and fire.

Thicket

The thicket vegetation described above presents a special problem of interpretation. The species involved are basically those of the middle and lower levels of successional stage four woodland, as described above, yet their formation is very much more dense. We believe that the thicket is formed after the taller vegetation in successional stage four has been removed by fire. With less competition for light and ground moisture, the lower bushes and shrubs grow together in a tight closed formation. Undistrubed long enough the former taller trees may emerge through the thicket and re-establish a woodland, and without further fire disturbance continue on the normal succession.

*13 Evidence for this interpretation comes from several sources. One is the series of tsetse clearings in the former woodland near Aitong and the Mara Ranch. The original vegetation according to the records was a

*13 successional stage four. Large areas were cleared by mechanical means and by burning. The first clearings were in the early 1950's, and the latest in 1961. The vegetation that had regrown in the old clearings, and that was regrowing in the new ones (except for areas where there was reburning and recutting) was typical thicket formation.

Additionally, in the old thicket formations in northern Tanganyika there are many places where the successional stage four trees were growing up through and somewhat opening the thickets, creating stage four conditions again.

Ant (termite) hills are frequent in the thickets, and the deep dissections of game trails create a *137 waffle-like relief under the thickets (Fig. 86). In larger thickets the vegetation is uniform on top of and around the base of these high spots. We examined many to assure this. The sides of the hillocks often have a grass cover which is heavily grazed, forming a fire break. When fire enters these thickets it burns through on the level, leaving little patches of thicket on the hummock and ant hill tops. The grass is ordinarily low around the thickets due to grazing, and the light fires that enter them singe the vegetation on the

[TEXT CONTINUED ON PAGE 398]

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Figure 86.

Vertical view of thicket (in central foreground) illustrating dissection of thicket by animal trails.

*137 hillocks but often do not kill it. Gradually through burning the thicket becomes smaller and smaller, leaving little outlying pieces of thicket vegetation on top of hillocks (Fig. 87). These relic thickets protected by fire breaks are often all that is left of former large thicket formations, and many observers have assumed this vegetation to be a community unique to ant hills without realizing its true origin.

In December of 1959 we marked one thicket that was about 200 yards wide and nearly one half mile long. Our track went across the middle of it and the vegetation was so thick that it scraped the vehicle. By June, 1961, fires had so opened the thicket that the only woody vegetation remaining was on the occasional hillocks, 10 to 25 yards from our track.

We have never seen an actively expanding thicket. Most thickets were being opened by fire and wild animals, and many had dead plants in them. Being originally undergrowth, the thickets apparently relied on taller vegetation for shade and some protection from desiccation. When this was removed, they appeared to compensate for it to some extent by their close growth form. These close thickets apparently can maintain themselves, but not

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Figure 87.

Hill top thickets in foreground were originally one long thicket. Fire has reduced the thicket, dividing it into several smaller patches and leaving small patches of thicket vegetation isolated on anthills, protected by the bare trampled and grazed fire break that shows as a light colored ring around them. In the background are strips of riverine forest and more thickets, with ant hill patterns showing on hills.

*137

expand, and they are quite vulnerable to fire and desiccation.

Summary and Conclusions

Most vegetation types in Western Masailand are the result of the interaction of normal vegetation succession, fire, and grazing. Except for relic patches of forest there is almost no vegetation type in the study area that represents a successional stage unmodified by fire and grazing.

OUTLINE OF THE ECOLOGICAL HISTORY OF WESTERN MASAILAND

*126 Methods

This interpretation is based on two sets of data. The first comes from our field work. It is clearly possible to determine the recent grazing history of an area from examination of its present condition. It is merely one step farther to carry such a determination to a longer period when woody vegetation is involved.

When we had learned the patterns of vegetation succession and their influences, it became apparent that there had been considerable changes in the vegetation of the study area within the past century. Cedar forest, for example, clearly covered a much larger area in the recent past and the stumps were there to prove it. Much of the closed woodland or bushland north of the Serengeti had been relatively open grassland, judging by the pattern and age of the woody formations. Consequently we made a map of what the vegetation of the area should have been about fifty years ago.

127 Several months later, while searching through the library of the Geological Survey Department at Dodoma, Tanganyika, we came upon a copy of the supplement to Jaeger's work of 1913. In it were his

(27 maps, including his vegetation map which we had not known existed. This map covered the study area from the Ngorongoro Highlands north into the Loita Plateau and the Mara Plains. The exciting thing was that it looked like our reconstruction.

Our second set of data basic to the ecological history that follows consists of a series of pieces of information gathered from the various sources cited above. Jaeger's map is the most complete, but we have tried to gather evidence from a number of other sources to confirm or modify our field interpretation. Fortunately, the available data appears to confirm it.

One example illustrates the oblique way we have come upon key pieces of information.

Grant (1957) while discussing Masai administrative boundaries notes that a German boundary is based on a hill plotted on their map that does not exist on the ground. The hill involved is called Nyamagati and is shown to be in the northern part of the open Serengeti Plain. We knew of no such hill, and Grant for several years was a District Officer in charge of that part of Masailand so he should know. Yet we had found German maps consistantly accurate in other matters. Consequently

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we collected maps to check on the matter.

The German map to which he refers (German East Africa Series, 1915), shows a Njamagati hill or promentory with a spring. This point is also shown on the very accurate map of Jaeger (1913) and is carried on the 1946

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127 War Office map of the area. On two more recent sketch maps (Geol. Surv. Dept., 1959; Swynnerton, 1957) a kopje or inselberg called Soit a (or e) Motonyi appears in the area. The most recent survey of the area (Geol. Surv. Dept., 1958) shows a Soit le Motnyi kopje but 3.75 miles north east is an apparently larger kopje in the precise coordinates shown by Jaeger (op. cit.). We have camped at that kopje. It once had a spring but most of the vegetation of the kopje has been cut or burned and the spring was dry when we visited it in 1956, 1960, and 1961. But today the kopje is in a thick Acacia woodland, not in the open plains. Because of the trees it is hard to see until one is almost at it. With a clear view unobstructed by Acacias the kopje would be a significant landmark. And this it was when the Germans came this way. According to Jaeger (1913) when he visited this area there was open grass steppe for about 18 miles airline north of the kopje. Now this whole area is a closed Acacia woodland.

*137 Historical Outline

Before 1850: In the very distant past the whole of Western Masailand, with the possible exception of part of the eastern Serengeti Plain, *could have been* under moist forest. In recent centuries there has probably been a gradual retreat of the moist forest up the hills and mountains and to the vicinity of the rivers. The rest of the area has probably seen a series of alternations between open grassland, bushland, and woodland. A cedar forest probably succeeded the moist forest and certainly existed throughout much of the region above about 6,000 feet elevation. The flattest areas supported the largest open grasslands, and probably saw a series of fluctuations in the amount of woody vegetation within them
*13 and in their extents. The obvious factor controlling these fluctuations is fire, and it would be affected by the amount of available fuel, therefore, by the intensity of grazing by ungulates and by frequency and distribution of ignitions.

Mid-1800's: The Il Datwa and the Masai who drove them out both grazed cattle. The Masai, at least, occupied the southwest part of the plains (Grant, 1957). That area, then, must have been open enough to exclude tsetse fly. There was probably open woodland ranging to an orchard steppe bushland throughout many parts of what

*137 is now open grassland in the Serengeti Plain. The region of Olduvai, Lake Lgarya, the various groups of kopjes, and the Ol Donjo Gol Mountains (in the east between the Serengeti and Salai Plains) were all well wooded from present evidence and Masai occupancy. The numerous watercourses in the open plains also must have had at least an open woodland within them. There are still stumps and occasional trees in all these areas. In 1956 there were open lines of trees in watercourses in the eastern Serengeti Plain where by 1960 all were gone.

*137
101 To the north the Masai occupied the Loita Plateau and the Loita Plain. The plateau and the hills to the north were called by the Masai Osobogo lo Loita or Osubogo lo Loiitai (German East Africa, Ikoma A 4) which means rain forest of the Loita, just as the Ngorongoro Highlands were known as Osobugo lo Datwa, rain forest of
*137 the Datwa (Grant, 1957). Relics of broad leaf forest still exist on the plateau and hills, along with what is left of a cedar forest. Much of the Loita Plain was probably open grassland, but the cedar forest extended far out into it in the north and open or closed woodland existed in many parts.

*136
*137 The area to the west, including the Mara Plains and Tanganyika south to the Serengeti Plain was not infested

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*[136] by tsetse fly -- so must have been relatively open.

[101] [231] *[233] 1850-1890: This appears to have been a period of increased burning, expansion of the Masai into the lands north of the Serengeti up to the Mara Plains, and increasing numbers of livestock. The open grasslands reached their greatest extent during this period, and the area between the Serengeti Plain and the Mara became open grassland with riverine forest and scattered thickets, much like the present southern Mara Plains (Fig. 79a).

*134 137 [101] The Masai apparently extended their grazing and particularly burning far up into the Mau Escarpment. Spectacular erosion can be seen over much of the Mau Escarpment, north and east of the Loita Plain. Virtually no top soil can be seen over hundreds of square miles at the lower elevations, and where some does remain it may be 10 to 14 feet above the present ground level, on top of a pedestal of earth held against erosion by the roots of a few surviving cedar trees. Trees growing in the bottom of these erosion scars in 1960 were dated as being 50 to 80 years old which would put the period of recovery in the late 1800's at or after [101] the disasters of the Masai. During the period of dry years culminating in 1961 the Masai extended their

134 *137 [101] burning and grazing far up into the same area of the forest, and the torrential rains that followed the dry period in 1961 created new erosion scars of as great magnitude as those of the earlier period.

*13 *233 [731] At the peak of the power of the Masai in the 1880's they had very large numbers of livestock. Their peak of intensity of livestock grazing, and probably overgrazing, came at the onset of the droughts which culminated in the famine of 1890. Conditions may have been much the same as in 1961. The effect of grazing animals on the vegetation, as well as the impact of fires where there was fuel, probably reached a peak about 1890. It is probable that a brush invasion through overgrazing was already starting in some of the open grassland.

[101] 1890-1918: The result of the combination of disasters that struck the Masai in the 1890's was that they largely vacated the Serengeti Plain and the country to the north all the way to the Loita Plain. There was a period of about 15 years of very much reduced grazing by domestic livestock and apparently reduced grass burning, and for part of this period there was probably almost no regular grazing or burning. This was

*13
*233 a period of increase in woody growth. The area was still burned on occasion by the Wanderobo. In 1906 when Jaeger visited it the boundaries of the open Serengeti Plain were wider than now, and the country to the north was still largely open. As the bush increased the tsetse flies moved in from the infested areas south and west. Figure 27[!] shows the spread of the fly during this period.

[!] [See p. 194.--Analyst]

[(a)] 1918-1962: After the first world war the Masai were allowed and encouraged to re-occupy Western Masailand. Burning and grazing were continued, but grazing was limited by the tsetse fly which continued to spread north. The effect of the frequent burning was apparently to stabilize the invading woody growth in the areas occupied by tsetse fly. From the 1920's to the present the general aspect of the bush country between the Mara and the Serengeti Plain has little changed. Examination of it shows clearly the stages that preceded the present stage.

137* Figure 88 is a general view south into the bush country of northern Tanganyika adjacent to the Mara Plains. During the Masai occupation prior to 1900 the burning and grazing restricted woody vegetation to riverine forests and scattered thickets, with occasional areas of open woodland. Then Whistling Thorn and other

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Figure 88.

View south into northern Tanganyika from the Kenya border near the Mara Plains. The pattern of thorn tree occupation of former open grasslands around riverine forest and thickets is clearly illustrated.

*(37 similar growth invaded the grasslands. Subsequent burning, modified by the grazing of wild ungulates, has somewhat stabilized the invading thorn trees in a thin bush or woodland which fills the former open grassland surrounding the thickets, riverine forest and taller woodland. To some extent the invading thorn trees have been cleared from the flats near the watercourses. As described above, such areas tend to support hotter fires. Most of these areas did have Acacias since stumps are frequent.

[23] With the increasing numbers of their livestock,
[178] the Masai have tried to clear as much land as possible
*[258] for pasture. Their extensive burning, plus elephant damage in the Mara area, has been rapidly reducing the woody vegetation during the past 20 years or so. Their burning has been restricting the range of the tsetse fly in the north. Yet while they are reducing the larger woody growth, the smaller growth such as Whistling Thorn is rapidly increasing on many of their grazing lands. On the Mau Escarpment their fire-created increases in grazing land at the expense of the cedar forest are being off set by expansion of the land covered by leleshwa bush, which invades overgrazed, underburned grassland in cedar forest areas in much the same way Whistling Thorn invades lower grasslands.

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[231]
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Also as the herds of domestic livestock have increased the entire area available for their grazing has become seriously overgrazed. Every area of tall grass plains available to the Masai has been overgrazed into short grass plains, weedlands, brushlands, or semi-desert.

The movements of the migratory wild ungulates through the area are strongly affected by the effects of fire and grazing. When the area south of the Mara Plains does not burn, the strip of tall dry grass provides a barrier for most forms of wildlife and the Kenya animals are effectively separated from the Tanganyika ones. During the pre 1890 period there was probably a much freer movement of wildlife through the then-open lands between the Mara and the Serengeti Plains.

The overgrazing-induced short grass plains have affected some animals' distributions. We have found that topi, for example, are limited to tall grass plains. Their present distribution in Western Masailand is precisely limited to the tall grass areas. Yet in the early 1900's White (1915) recorded them in the Loita Plateaus around and west of Loliondo, and east of the Guaso Nyiro River.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

*13 The wild ungulates utilize the combination of open grass plains and more wooded dry season grazing areas to maintain their high biomass. They are less common in dense bush or woodland where they do not have access to open grasslands, few exist in true forests, and few can exist yearlong on open grasslands. The present abundance and variety of wild ungulates is closely associated with the mixed open grassland - woodland complex and cannot apparently exist without it.

MAN'S ROLE IN THE GRASSLAND ECOSYSTEM

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The Masai are not now and probably never have been in a real equilibrium with their environment. Their history as we know it can be interpreted as roughly parallel to a part of the Americans' exploitation of the United States; exploiting a bit of land and then moving on west until there was no more land to the west.

[178]
[177] The exploitation of land by the Masai was a very long term process until the advent of the Europeans. The combination of peaceful administration, veterinary services, and matches have greatly accelerated the rate of exploitation, but they do not appear to have altered the basic processes. The only difference is that this time the Masai have no more land to the west.

It would be interesting to know if this basic lack of equilibrium with the environment was common to other pastoral tribes in Africa and especially those who preceeded the Masai.

As described and discussed above, the grassland ecosystem in Western Masailand, including its wild fauna, is maintained -- and created -- by a combination of

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grazing and burning. We have no evidence of fires in the area lit by any agency other than man. Fires might be started at rare intervals by Lengai Volcano. They might be ignited by lightning. But if the climatic regime of the past 20 years or so is typical, lightning fires must be exceedingly rare. Creation and maintenance of the grassland ecosystem requires frequent burning. The inescapable conclusion is that man is very closely associated with the origin and maintenance of the ecosystem.

This conclusion is obvious and not new. Swynnerton in 1936 (p. 464) discussing the spread of tsetse files wrote:

> The wooded savannas which cover east Africa today are essentially the product of a cultivating, grass-burning man. Few fires are lighted by nature, and fewer still can have arisen when the whole country was under the cover of the evergreen forest and deciduous thicket which evidently preceded so much of the savanna and which today succeeds it when we exclude the grass fires. Whether our savannas originated before the advent of man or after -- perhaps many thousands of years ago in a man-settled Sahara with a moister climate than today -- none can say. It can, however, be said with some confidence that _G. morsitans_ and _G. swynnertoni_, the two tsetse species that essentially belong to savanna, owe their present distribution to man.

*13
Yet there is a curious reluctance on the part of many to accept the importance of human activities in shaping the landscape. H.C. Pereira wrote (pers. comm. 1961) that: "All ecologists agree that natural tree and grass savanna associations in Africa are stable climax

*13 covers."

This paper has been written by an ecologist who does not agree.

19: Talbot K-4,5 (1956-1962)1964 FL12 Masai FL12

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The field work in East Africa was made possible -- and extremely pleasurable -- by the friendly and generous hospitality, cooperation, help, and provision of facilities by many individuals and organizations. The privilege of meeting and working with so many people in East Africa has let to an increased understanding of the problems they face, to deep respect for the fine work they are doing in many fields, and to warm friendships. Indeed, these insights and relationships are to us an outstanding aspect of our project.

In Kenya our field work was carried out in close and friendly cooperation with the Kenya Game Department and many of our most pleasant memories of the study involve the Department and the many members with whom we were associated. X122 We are particularly grateful to Major Ian Grimwood, Chief Game Warden, for advice, hospitality, encouragement, and the very many facilities he placed at our disposal. Our deep gratitude is also due Col. Neil Sandeman, Assistant, and for a long time Acting Chief Game Warden. Other members of the Department to whom we owe thanks for assistances include Game Wardens B. Carter, A. Graham, K. Smith, and R. Winterburn.

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*114
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127 Although very little information was available on the ecology of the study area or its wildlife when the present study was initiated in 1956, brief ecological reconnaissances of two parts of the area had been carried out between then and 1959 when we started the major period of field work. The excellent report by Dr. Pearsall (1957) on his two month survey of the then

127 Serengeti National Park has proved very helpful in that part of the study area. The report by Dr. Darling (1960) on his ten weeks' reconnaissance in the Mara was not yet published when we left for Africa in 1959, but he very generously gave us a first draft. This wonderfully perceptive reconnaissance has veen of great value to us, and we are deeply grateful to Dr. Darling for giving us his report as well as for his advice, guidance, and encouragement throughout the study.

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*114

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[For information on the ecosystem and on different aspects of geographical description, *passim*, see category 116, pp. 13, 21-38, 57-64, 88-110, 130-132, 147-171, 275-279, and 288-415.]

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[For bibliographical citations, see Category 116, pp. 429-454.]

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[For comments, see category 116, pp. 11-14, 40-42, 65, 95-98, 210-225, 319, 349, 350, and 416-428.]

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SL12 Masai FL12

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[For information on practical preparations, passim, see category 116, pp. 11-49 and 416-425.]

19: Talbot

FL12 Masai FL12

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[For description of tests and schedules, passim, see category 116, pp. 42-48; 77-84; 198-252; and 319-324.]

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[For methods of recording and collecting information, passim, see category 116, pp. 42-65, 195-220, 237-239, 297, 319-324, and 401.]

19: Talbot

FL12 Masai FL12

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[For information on type of climate, see category 116, pp. 61-87, and 301.]

19: Talbot

FL12 Masai FL12

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[For topographical data, passim, see category 116, pp. 9-A -12, 17-68, 87-94, 194, 213, 266, and 328-409.]

19: Talbot FL12 Masai FL12

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[For information on native fauna, *passim*, see category 116, pp. 16-56, 155-372, 405 and 406.]

19: Talbot FL12 Masai FL12

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[For information on flora, *passim*, see category 116, pp. 16-22, 166, 197, 206, 240-258, 309 and 324-410.]

19: Talbot FL12 Masai FL12

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[For additional information on pastoral activities, see also category 231.]

19: Talbot FL12 Masai FL12

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[For information on pastoral activities, passim, see category 116, pp. 24-162, 251, 252, 310-315, and 349-411.]